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# TESTING RESISTANCE TO SHATTERING AND LODGING IN CEREALS[1]

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## INTRODUCTION

Over a period of years large annual losses are caused to the cereal crops of Western Canada by unfavourable weather conditions at harvest time. Wind, often accompanied by rain, causes shattering, stem breaking and lodging. The increased use of the combine for harvesting and the trend toward larger farm units result in crops often being left standing ripe for several weeks before they are harvested. Moreover, in an extremely favourable crop year, such as 1942, the abnormally large amount of grain to be harvested and the interference of wet weather with harvesting operations may result in tens of thousands of acres of crop being exposed uncut for long periods after the grain is ripe.

Many factors concern the ability of varieties to hold their grain in a recoverable position for a period of several weeks after maturity. While the problem is complex, shattering and lodging are so important commercially that any real improvement in existing methods of appraising varieties and selecting hybrids for shattering and lodging resistance should be of considerable value to both farmers and cereal breeders. Accordingly, a study was commenced in 1946 at the University of Saskatchewan with the financial assistance of the National Research Council. The present paper is a progress report on the first three years of work.

## LITERATURE REVIEW

The importance of root development in the resistance of plants to lodging has been emphasized by numerous investigators. Derick and Hamilton (4) and Caffery and Carroll (2) working with oats, and McRostie and MacLachlan (8), Hayes and McClelland (6) and Hall (5) working with corn, found strong root development with substantial anchorage was closely related to lodging resistance.

Many investigators have studied the culm of cereals to learn more about varietal resistance to lodging. Welton and Morris (10) considered carbohydrate content at heading time an important factor in determining the habit of growth and consequently a leading factor involved in lodging; Willis (11) found breaking strength of the straw related to lodging, and Atkins (1) found unit weight of straw sections to be as reliable an index as breaking strength.

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Various studies have been made on methods of testing shattering in cereals. Jung (7) estimated shattering from heads dropped on a glass plate. Vogel (9) and Chang (3) found that tightly attached glumes allowed less shattering to occur. Chang (3) also classified varieties for shattering after beating the heads in a special machine.

## MATERIALS AND METHODS

Varieties ranking from high to low for resistance to lodging and shattering were used in each crop with a total of 21 of wheat, 18 of barley and 10 of oats. Replicated sowings in different sized microplots at different dates and under different conditions, including irrigation, were made each year at Saskatoon. Various methods were devised and machines constructed to test single plants as well as entire plots for shattering and lodging. Of the 14 methods tested, 11 proved unsatisfactory and three showed distinct promise.

## METHODS PROVING UNSATISFACTORY

1. *The wind machine* is a device for exposing field microplots individually to a strong controlled wind caused by an aeroplane propeller driven by an automobile engine. This machine was used extensively for three years with various wind velocities and exposure periods. The results showed the device to have some value but on the whole to be too slow, cumbersome and limited by weather conditions to be worth-while.

2. *Hygroscopicity* of the chaff and grain were studied through the use of Petri dishes, dessicators, a large incubator and quantitative scales. These tests were comprehensive, yet gave no significant differences between varieties.

3. *Spikes rubbing together*, as in a wind, was achieved with a device in which the heads, fixed in upright positions, were caused to rub together. Although tried with many modifications, this machine proved quite unsatisfactory.

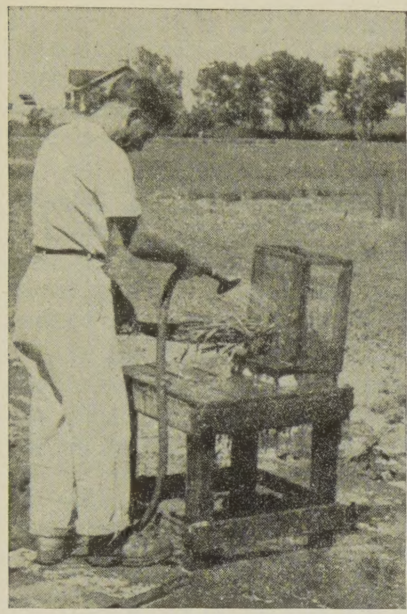
4. *Compressed air* was used to secure a vigorous agitation of heads in a metal cylinder, the air being directed into the cylinder by a nozzle. Various air pressures were used but the results did not agree sufficiently well with field shattering to be considered reliable.

5. *A corrugated wire drum*, in which heads of grain were tumbled about by hand crank rotation of the drum, gave results of some value. However, the work was very time-consuming and the device was considered impractical.

6. *A corrugated metal drum* lined with metal cleats and rotated by a hand crank gave results which agree fairly well with field performance; but the method was considered too time-consuming to be of practical value.

7. *Alternate wetting and drying* of heads in the nursery plots using a portable sprayer gave results of no value.

8. *Nutrient solution* tests in which several varieties of each crop were grown in gallon jars of nutrient solution in the greenhouse for comparison of root and crown development proved disappointing. The results suggested that a fibrous, much-branched root system was associated with lodging resistance, but the data were inconclusive statistically.




FIGURES 1 and 2. Root washing, preliminary and final stages.

9. *Lodging induced* by pressing each row of plants down with a board and then letting the material recover as best it could showed no correlation with the known lodging behaviour of the varieties tested.

10. *Culm weight.* Atkins' (1) method of weighing a hundred comparable stem portions of different varieties and correlating the weights with field lodging results was tested thoroughly. The tests were continued for three years but the results proved of little real value.

11. *Root pulling resistance* was obtained by tying a cord to a plant at its base and pulling it out vertically with a recording spring balance. In 1946, the first year of this investigation, significant varietal differences were obtained and the method seemed promising. However, in the two succeeding years, although the sampling and testing techniques were made as efficient as possible, the results were disappointing. The method was deemed unsatisfactory as a means of testing tendency to lodge.

## METHODS SHOWING PROMISE

1. *Glume pulling.* Strength of glume attachment was tested by Vogel's (9) method, which consists of using a small spring balance to loosen a glume. A preliminary study, in which ten heads of each of seven varieties were used, showed a general agreement between grams pulling resistance and the known shattering resistance of the varieties. A progressive increase in strength of glume attachment from the second to the basal spikelet was also apparent.

The method was then applied to all of the varieties of wheat with the results given in Table 1. The data show that in all varieties there was a general increase in glume strength toward the base of the spike. The strength of attachment of the glumes was greater in the durum wheat

TABLE 1.—THE NUMBER OF GRAMS PULL REQUIRED TO REMOVE THE GLUMES FROM EIGHTEEN VARIETIES OF WHEAT*

| Varieties | Spikelet number from top to bottom of spike | | | | | | | | | | | | Mean results for spikelets | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 2 and 3 | 9 and 10 | 2, 3, 9 and 10 | All |
| Pelissier | 23.4 | 24.2 | 28.2 | 32.3 | 36.2 | 41.2 | 41.5 | 51.5 | 51.1 | 60.8 | 64.9 | 63.0 | 26.2 | 55.9 | 41.0 | 43.2 |
| Mindum | 15.3 | 11.4 | 12.8 | 13.4 | 18.0 | 19.4 | 21.4 | 23.1 | 24.8 | 27.4 | 28.0 | 35.6 | 12.1 | 26.1 | 19.1 | 20.9 |
| Stewart | 22.0 | 15.2 | 22.2 | 25.0 | 26.0 | 28.0 | 32.8 | 37.5 | 39.1 | 41.2 | 45.0 | 53.6 | 18.7 | 40.1 | 29.4 | 32.3 |
| Thatcher | 29.8 | 7.7 | 8.5 | 10.2 | 12.8 | 12.6 | 19.0 | 23.3 | 28.1 | 31.7 | 33.7 | 38.5 | 8.1 | 29.9 | 19.0 | 21.3 |
| Marquis | 26.4 | 1.5 | 2.8 | 7.6 | 13.0 | 12.6 | 20.2 | 23.6 | 26.8 | 32.8 | 36.2 | 43.0 | 2.1 | 29.8 | 15.9 | 20.5 |
| Cadet | 32.5 | 6.6 | 8.1 | 9.5 | 16.0 | 16.5 | 21.4 | 25.5 | 27.9 | 25.6 | 26.2 | 25.6 | 7.3 | 26.7 | 17.0 | 20.1 |
| Apex | 24.5 | 1.4 | 3.2 | 7.0 | 8.8 | 13.4 | 16.8 | 23.8 | 26.8 | 28.2 | 32.4 | 33.2 | 2.3 | 28.0 | 15.1 | 18.3 |
| Renown | 22.4 | 1.6 | 4.0 | 6.0 | 11.5 | 15.4 | 23.4 | 29.0 | 36.2 | 38.9 | 42.2 | 47.2 | 2.8 | 37.5 | 20.6 | 23.2 |
| Reward | 15.8 | 1.0 | 1.2 | 3.2 | 5.5 | 8.7 | 13.0 | 15.2 | 23.4 | 27.0 | 29.9 | 33.6 | 1.1 | 25.2 | 13.1 | 14.8 |
| Regent | 14.4 | 1.4 | 2.3 | 3.5 | 5.1 | 9.1 | 11.4 | 14.6 | 18.8 | 20.4 | 21.7 | 21.2 | 1.8 | 19.6 | 10.7 | 12.0 |
| Rescue | 19.4 | 2.9 | 4.8 | 4.9 | 7.0 | 8.2 | 9.9 | 9.5 | 10.9 | 10.8 | 11.9 | 13.6 | 3.8 | 10.8 | 7.3 | 9.5 |
| Comet | 53.4 | 9.2 | 15.4 | 21.5 | 24.2 | 28.0 | 35.0 | 36.2 | 39.0 | 40.9 | 50.2 | 65.1 | 12.3 | 39.9 | 26.1 | 34.8 |
| Reliance | 35.4 | 12.0 | 17.3 | 18.8 | 19.1 | 23.2 | 25.4 | 29.6 | 32.7 | 36.1 | 33.4 | 41.6 | 14.6 | 34.4 | 24.5 | 27.1 |
| Red Bobs | 8.0 | 1.0 | 1.2 | 1.2 | 1.7 | 1.6 | 3.2 | 3.6 | 5.6 | 6.2 | 6.6 | 8.0 | 1.1 | 5.9 | 3.5 | 4.0 |
| Garnet | 16.0 | 1.0 | 1.3 | 2.6 | 4.5 | 5.0 | 7.5 | 8.3 | 12.8 | 13.6 | 14.4 | 12.4 | 1.1 | 13.2 | 7.1 | 8.3 |
| Huron | 12.6 | 1.9 | 3.2 | 5.4 | 5.7 | 7.6 | 8.6 | 9.8 | 11.0 | 11.9 | 12.7 | 14.7 | 2.5 | 11.4 | 6.9 | 8.8 |
| Pioneer | 15.6 | 1.0 | 1.3 | 1.6 | 1.6 | 3.5 | 4.6 | 5.0 | 5.9 | 7.2 | 7.6 | 8.1 | 1.1 | 6.5 | 4.3 | 5.2 |
| Mercury | 35.8 | 4.4 | 6.6 | 8.8 | 9.8 | 14.4 | 19.2 | 22.4 | 22.5 | 26.6 | 23.0 | 21.0 | 5.5 | 24.5 | 15.0 | 17.9 |

* Each figure is the average for the first and second glume of the designated spikelet of each of ten heads.

varieties than in the common wheat varieties. In general the pulling resistance of the glumes agreed with the known shattering resistance of the varieties. However, there was some lack of agreement. For example, Thatcher, which resists shattering far more than Mercury, was similar to that variety in glume pulling resistance.

A study of the varietal differences for different parts of the head revealed that the average for the second and third spikelets from the top of the head together with the average for the third and fourth spikelets from the bottom, gave about as good a picture of varietal performance as the results from the entire heads. These averages are shown with the general averages in the last four columns of Table 1.

2. *The paddle device.* In 1948, a head-striking machine essentially similar to that described by Chang (3) was constructed. With this device ripe heads are subjected to the striking or beating action of a plywood paddle, actuated by a motor-driven eccentric. The weight of grain threshed out of thirty heads treated in groups of three was obtained for each of 18 varieties of wheat. The data, converted to percentage shattered, are presented in Table 2.

The shattering results of the paddle method did not agree exactly with the known behaviour of the varieties but the grouping of the resistant as compared with the susceptible varieties was good. This method is quite promising.

TABLE 2.—COMPARATIVE SHATTERING RESULTS ON WHEAT VARIETIES AS OBTAINED WITH VARIOUS LABORATORY AND FIELD DEVICES AND IN THE REPLICATED NURSERY PLOT TESTS

| Variety | Summarized* SRC** | Field shattering 1948, Saskatoon | | Strength† of attachment of glumes | | Shattering induced by paddle device | |
|---|---|---|---|---|---|---|---|
| | | Per cent | SRC | Grm. | SRC | Per cent | SRC |
| Pelissier | VH | 0.5 | H | 43.2 | VH | 0.0 | VH |
| Stewart | VH | 1.0 | H | 32.3 | VH | 1.9 | H |
| Mindum | H | 6.0 | M | 20.9 | H | 8.6 | MH |
| Thatcher | H | 1.0 | H | 21.3 | H | 3.3 | H |
| Saunders | H | 0.5 | H | — | — | 4.7 | H |
| Redman | H | 1.5 | H | — | — | 5.7 | H |
| Marquis | H | 2.0 | H | 20.5 | H | 10.6 | MH |
| Cadet | H | 2.0 | H | 20.1 | H | 13.1 | MH |
| Apex | H | 2.0 | H | 18.3 | H | 7.3 | MH |
| Renown | H | — | — | 23.2 | H | — | — |
| Reward | H | — | — | 14.8 | MH | — | — |
| Regent | H | 3.0 | MH | 12.0 | MH | 3.0 | H |
| Rescue | H | 4.0 | MH | 9.5 | MH | 9.3 | MH |
| Comet | H | — | — | 34.8 | VH | — | — |
| Reliance | M | 7.0 | M | 27.1 | H | 6.5 | MH |
| Red Bobs | ML | 2.0 | H | 4.0 | L | 10.3 | MH |
| Garnet | ML | 16.0 | L | 8.3 | L | 15.2 | ML |
| Huron | L | 25.0 | L | 8.8 | L | 22.2 | ML |
| Pioneer | L | 31.5 | L | 5.2 | L | 23.0 | ML |
| Prelude | L | 23.0 | L | — | — | 17.2 | ML |
| Mercury | L | 15.0 | L | 17.9 | MH | 57.0 | L |

* Using all available data for several years.
** SRC = Shattering Resistance Class.
† Average of primary and secondary glumes of each of the 2nd, 3rd, 9th and 10th spikelets from the top of each of ten heads.
*Abbreviations:* VH—Very high; H—High; MH—Medium high; M—Medium; ML—Medium low; L—Low.

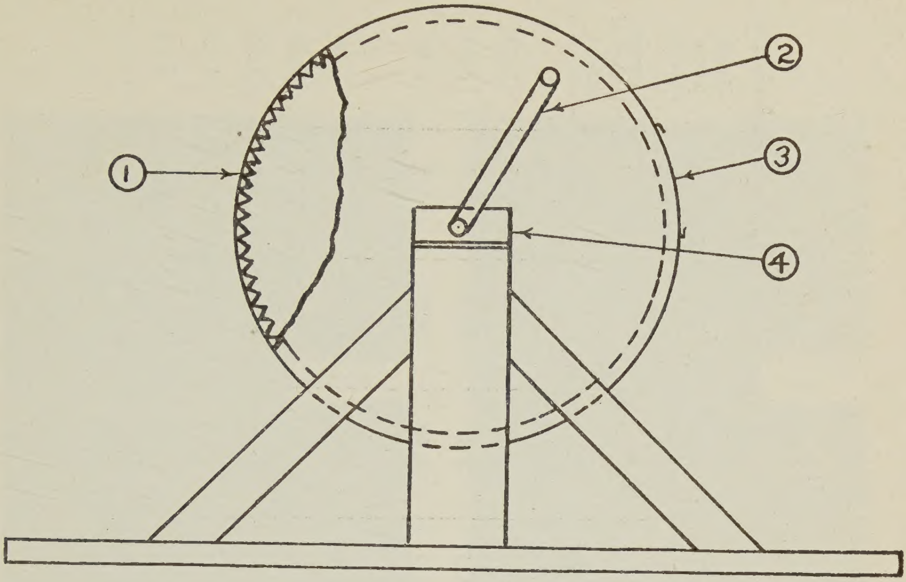
3. *Root washing method.* As a follow-up to the nutrient solution root studies of 1947, an experiment was devised to determine whether any relationship existed between root placement and lodging. Varieties representing a wide range of resistance to lodging were used, the seeds being sown 12 inches apart each way at a uniform depth. Ten plants in each of the following varieties were examined: Glacier, Newal, Vantage, Trebi, and Byng barley; Thatcher, Apex 1789, and Pioneer *vulgare* wheat; Carleton *durum* wheat and Prolific spring rye. The procedure used was to excavate a plant and its roots, taking up a block of soil one foot square and six inches deep. The block was placed in a wooden box and allowed to soak in water for several hours. A number of small, stiff rods were driven through each block from the side to prevent the roots from moving in one plane. The wooden box was then removed and the block was washed out with a fine spray. When washing was completed, the roots were flat upon a wooden plate. A comparative study of the roots showed no definite relation between root placement and the lodging resistance of the varieties concerned. In addition there appeared to be no correlation between the possession of a fibrous, much branched root system and resistance to lodging, although the preliminary greenhouse study suggested such a relationship.

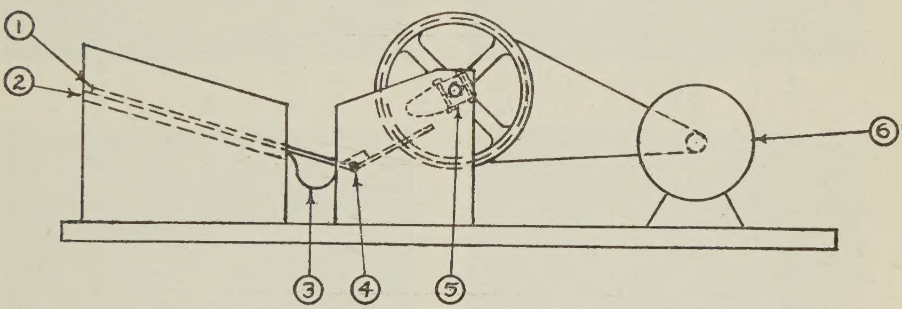
The second portion of the field experiment involved taking measurements of the following characters of the plants: height of the tallest culm; the average height of all culms; average culm diameter taken one inch above the second above ground internode; number of coronal roots; circumference of the crown; dry weight of top growth; dry weight of root growth. Indices were made of the ratio of the weight of top growth to the weight of root growth and of the ratio of crown circumference to the number of culms. The data for the ten plants of each variety averaged for each character are given in Table 3.

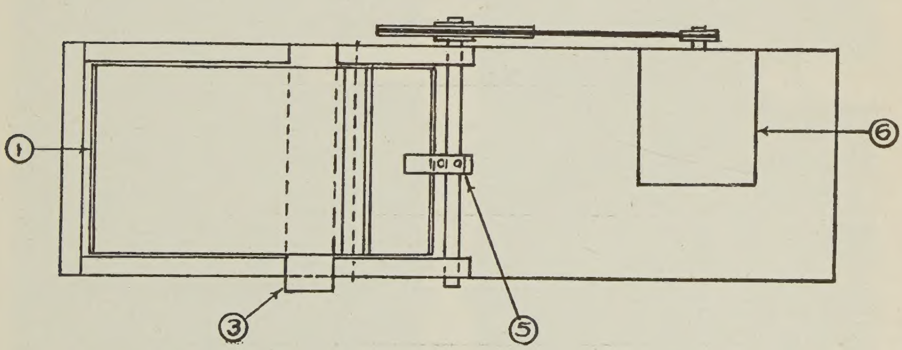
The results indicated a relationship between the number of coronal roots and lodging resistance, that is, the greater the number of coronal roots the greater the resistance to lodging. None of the other characters appeared to be correlated with lodging resistance. The variance analysis of the data on number of coronal roots showed highly significant varietal differences in wheat with Thatcher having more coronal roots than Apex and Apex more than Pioneer. Among the barley varieties there was a highly significant difference between the number of coronal roots of Glacier and of the two varieties Trebi and Byng and a significant difference (at the 5 per cent level) between Glacier and the varieties Vantage and Newal.

## DISCUSSION

Many environmental factors concern the ability of a variety to hold its grain in a recoverable position for a period of several weeks after maturity. This makes it extremely difficult to devise simple, quick tests which aid the breeder in differentiating varieties or hybrids as to this ability. The method used to obtain estimates of shattering or of lodging resistance must be suitable for different seasons and locations. Several of the various techniques and devices tested during the course of these investigations have proven of some value and at least three of them have distinct promise. However, most of them have been found to be too laborious or too unreliable for practical use.




FIGURES 3, 4 and 5.

*Top* (Figure 3)—Corrugated metal drum. (1) corrugations; (2) crank handle; (3) door, and (4) angle iron support and bearing.

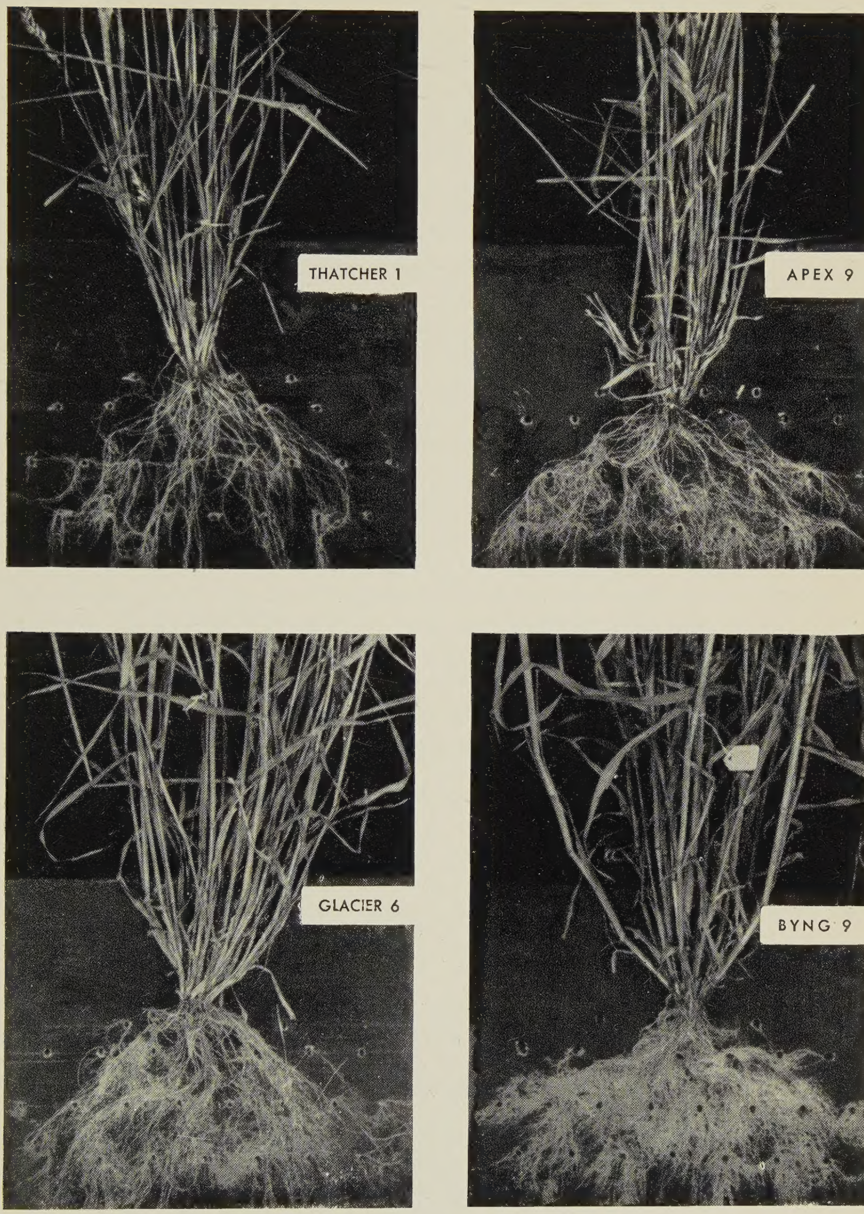
*Centre* (Figure 4)—Paddle device (legend as below).

*Bottom* (Figure 5)—Paddle device. (1) plywood paddle; (2) table; (3) metal trough; (4) pivot; (5) eccentric, and (6) electric motor.

TABLE 3.—SUMMARY OF DATA FROM CEREAL ROOT STUDIES

| Variety* | Average height of tallest culm (cm.) | Average height of all culms (cm.) | Average number of culms | Average culm diam. (mm.) | Average number of coronal roots | Average weight of top growth (gm.) | Average weight of root growth (gm.) | Ratio top growth / Root portion† | Average crown circum. (mm.) | Ratio crown circum. / Average number of culms |
|---|---|---|---|---|---|---|---|---|---|---|
| *Wheat* | | | | | | | | | | |
| Thatcher | 72.75 | 67.0 | 16.9 | 2.82 | 73.2 | 19.5 | 0.54 | 36.1 | 55.5 | 3.28 |
| Apex | 78.05 | 69.4 | 17.0 | 2.91 | 61.0 | 22.3 | 0.67 | 33.3 | 56.3 | 3.31 |
| Pioneer | 72.80 | 67.5 | 11.8 | 3.02 | 51.2 | 14.9 | 0.30 | 50.0 | 47.9 | 4.06 |
| *Barley* | | | | | | | | | | |
| Glacier | 70.90 | 66.7 | 15.1 | 3.78 | 67.0 | 23.3 | 1.82 | 12.8 | 61.8 | 4.09 |
| Vantage | 63.35 | 57.6 | 10.7 | 3.79 | 58.2 | 20.8 | 1.27 | 16.4 | 56.5 | 5.28 |
| Newal | 75.70 | 65.8 | 18.4 | 3.70 | 57.3 | 37.3 | 2.52 | 14.8 | 64.5 | 3.51 |
| Trebi | 60.50 | 55.7 | 14.3 | 3.47 | 54.5 | 22.5 | 0.82 | 27.4 | 59.4 | 4.15 |
| Byng | 76.90 | 66.3 | 20.1 | 3.72 | 54.5 | 32.8 | 2.37 | 13.8 | 63.2 | 3.14 |

† Weight ratio total top growth to portion of roots in soil 12 inches × 12 inches × 6 inches deep at plant's base.
* The varieties are arranged in order from the most to the least resistant to lodging according to nursery results, 1942 to 1948.




FIGURES 6 to 9. Representative plants of Thatcher and Apex wheat, and Glacier and Byng barley.

The results obtained on shattering indicate that this character is complex and is influenced by various factors and combinations of circumstances. The method of recording shattering, as carried on at Saskatoon for a number of years*, by taking notes on border rows or special plots left standing for several weeks after harvest, appears to be more practical than any of the methods proposed in the literature. Nevertheless, results with the paddle device and the pulling resistance of wheat glumes proved to be fairly closely related to the known ability of varieties to resist shattering. The results suggest that either the paddle device or the glume pulling test could be used with a large degree of success in separating varieties as to shattering propensity under conditions which make inconvenient or impossible the taking of after-harvest shattering notes in the nursery.

The studies on lodging reveal that this character is also complex and much affected by environmental influences. Of the different methods used to evaluate varieties for lodging resistance, apart from taking field notes under propitious circumstances, such as in an irrigated nursery, the coronal root counting procedure proved to be the most promising. This method, while involving digging up and washing out the base of the plant and the adjacent roots, seems to have real merit.

A study of the promising procedures brought to light in this research project indicates that each of them can be simplified for application to hybrid lines. By using fewer heads per sample in the paddle device and by estimating rather than weighing the seed dislodged from the heads, the procedure could be used economically on hundreds of head samples. This device, with some adjustment, appears suitable to use on barley as well as on wheat. The data on glume pulling resistance show that satisfactory representation of a variety glume adherence may be obtained from the pulling resistance of the glumes on the second and third spikelets from the top of the head together with that of the third and fourth spikelets from the bottom of the head, and that an eight or ten head sample per variety is sufficient. This abbreviated procedure is sufficiently quick and economical to be used for testing hybrid lines. Finally, the elaborate, painstaking method developed for ascertaining the placement and number of coronal roots can be simplified by taking a smaller soil block, washing it without incasing it or using the rods and omitting all measurements excepting the count of coronal roots. These changes would allow the method to be used on hybrid lines.

The investigations of the past three years as herein reported are to be followed up by detailed exploitation of the merits of each of the three promising methods.

## SUMMARY

1. Fourteen methods and devices were used in an endeavour to develop better procedures for determining the relative resistance of varieties of cereal crops to shattering and lodging.

2. Three of the methods showed promising results. These are: (a) determining glume pulling resistance to obtain an estimate of shattering resistance; (b) beating grain heads with a paddle to determine shattering resistance directly, and (c) counting the number of crown roots to obtain an indication of lodging resistance.

* Developed by the Field Husbandry Department, University of Saskatchewan, during the period 1940 to 1945.

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# THE DETERMINATION OF PHOSPHORUS IN SODIUM ACETATE EXTRACTS OF SOIL[1]

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## INTRODUCTION

The use of a sodium acetate solution as extractant in a system of rapid tests for available plant food constituents in soils was first introduced by Morgan (2) in 1935 under the designation of the "Universal soil extracting solution". Since that time, this solution has been used in soil fertility investigations by many workers in various parts of the world. In 1944, in a study of rapid microchemical soil tests, Peech and English (3) indicated that the "solution proposed by Morgan has certain desirable features not possessed either by solutions of strong acids or by solutions of neutral salts" and they presented details of improved chemical methods for the determination of constituents extracted from soil by Morgan's solution.

## PREPARATION OF EXTRACTING SOLUTION

In the determination of phosphorus in such extracts, the molybdenum blue colours are usually compared visually with those of a set of standards prepared at the same time. In this laboratory, it was desired to make the readings in a Klett-Summerson photoelectric colorimeter. While such a procedure may be slightly more time-consuming, it is more accurate and obviates the necessity of running standards with every series of determinations. It was observed, however, that the blank reading obtained when only the reagents were used was quite large and this lessened the accuracy of the determination, particularly with soils of low phosphorus content. Attempts were made to reduce the value of the blank reading in two ways: (1) by purification of the activated carbon used to remove soluble organic matter, by boiling in hydrochloric acid, keeping warm on the hot plate overnight and washing repeatedly by decantation with large volumes of distilled water; (2) by making the extracting solution from sodium hydroxide and glacial acetic acid rather than from the sodium acetate salt. That these treatments were successful in reducing the magnitude of the colorimeter reading for the blank is shown by the following results, where the molybdate reagent used was made up in hydrochloric acid and stannous oxalate was used as the reducing agent:

Reading for solution made from $NaC_2H_3O_2 . 3H_2O$, using unpurified carbon—39;

Reading for solution made from $NaC_2H_3O_2 . 3H_2O$, using purified carbon—27;

Reading for solution made from $NaOH + HC_2H_3O_2$, using purified carbon—12.

It has been found that the value of the blank does vary between different lots of sodium acetate. Greater accuracy in the determinations can be expected when a low blank reading is obtained.

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### INTERFERENCE BY ARSENIC

One difficulty in all phosphorus determinations which depend on the development of the molybdenum blue colour is due to the fact that arsenic, when present in the arsenate form, gives the same colour. In many soils, particularly those from areas where arsenate spray residues have accumulated, this leads to somewhat high values for phosphorus. However, it has been shown (4) that arsenic in the arsenite form does not give a blue colour and this has suggested a means of eliminating the arsenate interference by reduction before the colour is developed. This reduction can be done by means of sodium bisulphite and this has been used by several workers (5, 6) under varying conditions.

In a proposed method for the determination of the total phosphorus content of a soil in which extraction is made with 60 per cent perchloric acid, Sherman (5) stated that the development of the blue colour is affected by acidity, temperature and time, and recommended a minimum of 2.5 ml. of perchloric acid in a 25 ml. volume and a temperature of $25° \pm 4°$ C., with readings being taken between 15 and 25 minutes after the reagents were mixed. When arsenic was present, solid sodium bisulphite was added and the solution allowed to stand for three hours before the colour was developed, using aminonaphtholsulphonic acid as reducing agent.

In this laboratory, the Sherman procedure has been modified so that it can be used in measuring the phosphorus extracted from a soil by Morgan's solution. To a suitable aliquot of the extract, 2.5 ml. of perchloric acid is added, followed by dilution with water and cooling. Sodium bisulphite is then added in solution and the mixture allowed to stand overnight. In the morning, the aminonaphtholsulphonic acid and ammonium molybdate are added and the colour read after 15 minutes.

When the sodium bisulphite was added in the solid form, a turbidity was obtained, necessitating centrifuging before the final development of the colour. When this compound was added in solution, no such turbidity was obtained. The making of a solution requires only one weighing and the measurement of a definite volume for each determination is relatively simple and rapid.

The importance of having the reaction of the solution in which the colour is developed sufficiently acid has been stressed by Holmes and Motzok (1) who have indicated that measuring acidity in terms of pH value rather than normality is preferable. It was shown that, when aminonaphtholsulphonic acid was used as the reducing agent, the range of acidity should be between pH 0.05 and pH 0.60, and this finding has been substantiated by work in this laboratory. In the procedure outlined below, the pH value of the final solution is approximately 0.35.

### DETAILS OF PROPOSED METHOD

The details of the modified method are as follows:

*Reagents*

*Extracting solution.* Dissolve 58.54 gm. of NaOH (C. P. grade) in water. Cool. Add 145.8 ml. of 99.5 per cent acetic acid. Make to 2 litres. If necessary, adjust to pH 4.85.

*Activated carbon.* Darco G 60, purified by boiling with 6 N HCl, keeping warm on the hot plate overnight, and washing repeatedly by decantation with large volumes of distilled water. The carbon is recovered from suspension by filtering on a Buckner funnel. It is then dried at 118° C. overnight.

*Perchloric acid.* Seventy-two per cent, phosphorus-free.

*Sodium hydrogen sulphite solution* (15 per cent)—Dissolve 15 gm. $NaHSO_3$ in distilled water, filter and make to 100 ml.

1,2,4-*Aminonaphtholsulphonic acid.* Add 0.25 gm. of this material to 88 ml. of 15 per cent $NaHSO_3$ solution. Then add, slowly and with shaking, a 20 per cent solution of sodium sulphite ($Na_2SO_3$) until the solution is clear. (This usually takes from 5 to 7 ml. Up to 4 ml. can be added in 1 ml. portions, the remainder drop-wise.) Filter and store in a dark bottle. Prepare fresh every week.

*Ammonium molybdate.* Dissolve 5 gm. $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$ in 100 ml. distilled water. Let stand overnight. Filter if necessary.

*Standard phosphate solution.* Dissolve 0.4390 gm. $KH_2PO_4$ in 1 litre of extracting solution. This solution contains 100 p.p.m. P. Dilute 100 ml. of this to 1 litre to make a solution containing 10 p.p.m. P.

*Procedure*

To 10 gm. of soil (air-dried and screened through a 2 mm. sieve) in a shaking bottle, add $\frac{1}{4}$ measuring teaspoonful ($\frac{1}{4}$ gm.) of purified activated carbon and 50 ml. of the extracting solution. Shake for 30 minutes and filter into a 50 ml. Erlenmeyer flask through a dry 15 cm. Whatman No. 42 filter paper.

Transfer 10 ml. of filtered extract (representing 2 gm. of soil) to a 50 ml. glass-stoppered graduated cylinder. Add 2.5 ml. of perchloric acid and mix. Dilute with distilled water to a volume of 18 ml., mix and let cool. Add 2.5 ml. of 15 per cent $NaHSO_3$ solution, mix thoroughly, stopper and let stand overnight.

Add 0.8 ml. of 1,2,4-aminonaphtholsulphonic acid solution and mix. Add 2 ml. of ammonium molybdate solution, and water to a volume of 25 ml. Mix thoroughly. Allow 15 minutes for the development of the colour and read in a photoelectric colorimeter, using a red filter.

Calculate the amount of phosphorus from a curve prepared as follows: Measure aliquots (100.0, 80.0, 60.0, 40.0, 20.0, 10.0, 5.0, 0.0 ml.) of the standard (10 p.p.m. P) phosphate solution into a series of 100 ml. volumetric flasks. Dilute to the mark with extracting solution and mix thoroughly. Pipette 10 ml. of each into 50 ml. glass-stoppered graduated cylinders and continue as in the second and third paragraphs under "procedure".

## ELIMINATION OF ARSENIC INTERFERENCE

The effect of arsenic on the apparent soluble phosphorus content of a soil, and the elimination of this effect by the procedure outlined above, is shown by the following experiment. Two soils well supplied with phosphorus soluble in the Universal extracting solution were treated in the

laboratory with increasing amounts of "insecto" containing 6.5 per cent As as calcium arsenate ($Ca_3(AsO_4)_2$). After moistening and drying, the samples were extracted in the usual manner and the phosphorus in the extract determined both with and without treatment with sodium bisulphite to eliminate the effect of the arsenic. The results obtained are presented in Table 1.

It is readily seen that, with both soils, increasing amounts of arsenic have resulted in increased values for the apparent phosphorus content when no sodium bisulphite was used. However, when the arsenic was reduced, the values for all five samples of each soil were approximately the same, indicating that the effect of the arsenic had been eliminated. In the the case of soil B, these values were about the same as that for the sample to which no arsenic had been added and where the colour was developed without the use of $NaHSO_3$. With soil A, however, the values obtained when $NaHSO_3$, was used were somewhat lower than that for the sample receiving no added arsenic and where no $NaHSO_3$ was used. This suggests the presence of arsenic in the original sample of soil A and this may well have been the case, since the sample was taken from an area on which potatoes have been grown frequently during the past 15 years and where arsenate spray residues may have accumulated.

## SUMMARY

In the colorimetric determination of phosphorus in soil extracts, care should be taken to eliminate interference by arsenic which gives a blue colour similar to that due to phosphorus. This can be done by reducing the arsenate to the arsenite form before development of the colour. A procedure for determining phosphorus in the presence of arsenic has been adapted for use with the sodium acetate (Universal) soil extracting solution. Data are presented for soil samples to which arsenic has been added, showing that the proposed method is satisfactory.

Table 1.—Determination of phosphorus in extracts of soils to which arsenic was added

| Soil | Arsenic added (p.p.m.As) | Apparent phosphorus content (lb. P per ac.) | |
|---|---|---|---|
| | | Without $NaHSO_3$ treatment | With $NaHSO_3$ treatment |
| A | 0 | 34 | 25 |
| | 10 | 37 | 25 |
| | 20 | 41 | 25 |
| | 40 | 54 | 26 |
| | 60 | 68 | 28 |
| B | 0 | 33 | 30 |
| | 40 | 41 | 32 |
| | 60 | 52 | 32 |
| | 80 | 56 | 33 |
| | 100 | 76 | 35 |

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# THE USE OF MONOSOMES AND NULLISOMES IN CYTOGENETIC STUDIES OF COMMON WHEAT[1]

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## INTRODUCTION

Viable chromosomal aberrations involving the loss of a portion of a chromosome, an entire chromosome, or even a chromosome pair provide a method of associating genes with certain chromosomes in some and possibly most polyploid species. This report deals with the use of 17 different nullisomic lines of common wheat in studying the genetics of glume colour, awning, spike density, habit of growth, leaf rust reaction and bunt reaction.

## REVIEW OF LITERATURE

### Cytologic and Cytogenetic Studies of Deficiencies for Whole Chromosomes, Pairs of Chromosomes, and Chromosome Arms

*Cytologic Studies of Monosomics*

Monosomics are plants deficient for an entire chromosome, and they have been obtained in several polyploid species. In *Nicotiana tabacum*, Clausen (15) reported obtaining 20 of the possible 24 monosomics and demonstrated their usefulness in associating genes with whole chromosomes. Transmission of whole chromosome deficiencies was studied by Olmo (41) in *N. tabacum* and by Lammerts (30) in *N. rustica*. In both species the deficiency was found to be transmitted with a high frequency through the eggs but only rarely through the pollen.

Whole chromosome deficiencies in common wheat have been reported by numerous investigators. However, the chromosome involved usually was associated with speltoidy of the B type (26, 36, 71). Love obtained several different monosomics in progenies of crosses between *T. durum* and *T. vulgare*. Kihara (29) found monosomics in derivatives of *T. polonicum* × *T. spelta*, and described the behaviour of univalent chromosomes at meiosis. Nishiyama (40) studied transmission of the deficiency in crosses between 2 different nullisomics with *T. spelta* and found 73 per cent effective female and 11 per cent effective male gametes to be n-1. Powers (45), and Myers and Powers (37) reported that meiotic instability and genetic irregularities often were associated with the monosomic condition.

*Cytologic Studies of Nullisomics*

Nullisomics are plants deficient for a pair of chromosomes. None was obtained by Clausen (15) in *N. tabacum*. Lammerts (30) suggested that viability of n-1 gametes and 2n-2 zygotes is evidence that a species is highly polyploid.

Nullisomics, obtained in the progeny of heterozygous speltoids, have been described in detail elsewhere (26, 36, 71). A few nullisomes, other than those resulting in speltoidy, also have been found (29, 33).

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It remained for Sears, however, to obtain a considerable number of different nullisomics in one variety. In his first of a series of papers (50), the origin of the deficiencies was related. They were obtained by pollinating a haploid plant of Chinese Spring with normal pollen. He postulated 4 ways in which the deficiencies could have arisen, and suggested that these deficiencies could be used for associating with specific chromosomes some of the genes of common wheat. Later (51), he reported briefly on 7 nullisomics obtained up to that time. All exhibited reduced vigour and fertility, but all were female fertile, and 4 produced functional pollen. Nullisomic line III, which was partially asynaptic, was suggested as a probable source of additional deficiencies. In 1944 he gave a comprehensive report (52) on 17 different nullisomics then available. He numbered the nullisomics I to XI in the order in which they were obtained if the nullisome corresponded to a particular chromosome of the Emmer (tetraploid) wheat series. Those that corresponded to a particular chromosome of the C genom of the common (hexaploid) wheats were numbered XV and up in the order in which they were obtained. He found that nullisomics represented from 0.9 to 10.3 per cent and monosomics 75 to 85 per cent of the progeny of the different monosomics.

*Cytologic Studies of Plants with Telocentric Chromosomes and Isochromosomes*

Telocentric chromosomes are deficient for an entire arm and have a terminal centromere. Isochromosomes are deficient for one arm and reduplicated for the other. Darlington (17) has shown that telocentric chromosomes were formed by misdivision of the centromere, and isochromosomes from the reduplication of such broken chromosomes.

The usefulness of a telocentric chromosome has been demonstrated in genetic studies of maize by Rhoades (47). Smith (56) indicated how they could be used in linkage studies of *T. monococcum.* Love (34) showed that telocentric chromosomes resulted in two different off-type "mutants" in the variety Dawson's Golden Chaff. In the case one mutant, the arm lost normally carried the gene for red chaff in that variety, since plants homozygous for the deficiency had white chaff. He believed these aberrations to be quite stable in common wheat, contrasting with the situation in maize (47). The function of telocentric chromosomes and isochromosomes, in changing plants from normalcy through speltoidy to compactoidy at various dosage levels, has been discussed by Sanchez-Monge and MacKey (49), and Li *et al.* (31). Sears (52, 53) found that isochromosomes and telocentric chromosomes frequently occurred in the progeny of certain monosomics. In somatic tissue, telocentric chromosomes were found to be less stable than isochromosomes. The latter had approximately the same frequency of loss and misdivision as primary monosomes.

*Cytogenetic Studies with Chromosome Deficiencies*

Sears (52) used monosomes to determine the location of certain genes. He found that a gene for red seed in Chinese Spring was carried by chromosome XVI. The B-type of speltoidy was associated with chromosome IX. Genes influencing awning were associated with chromosomes VIII, IX and X. In a later study (54) he associated the *sphaerococcum* gene with chromosom XVI. He found that when this recessive gene was in the

hemizygous condition, as was the case in the $F_1$'s of the cross nullisomic XVI × *T. sphaerococcum*, the sphaerococcum character was not exhibited. Two doses of the gene, therefore, were needed for the development of this character. Sears and Rodenhiser (55) associated two complementary genes for resistance to stem rust with chromosome X of the variety Timstein. O'Mara (42), by using these deficiencies, was able to associate three major awn-inhibiting genes with chromosome VIII, IX and X. He concluded that the series of genes for awning in common wheat was now complete. Unrau and Swenson (68), in a preliminary report of the present study, showed the association of a number of genes with certain chromosomes.

## Genetics of the Characters Involved in this Study

### *Glume Colour*

Genetic studies have indicated red or brown glume colour to be dominant over white. Both monohybrid (13, 14, 18, 10, 60, 61, 62, 63, 73) and dihybrid (67) ratios have been obtained.

### *Spike Density*

Apparently one main gene is responsible for differentiating "club" and "common" spikes in wheat (59, 19, 18, 60, 61, 62, 63, 65, 6). Most investigators also observed transgressive segregation in the material studied. Nilson-Ehle (39) explained such segregation with the hypothesis that there was a main gene, C, for club spikes epistatic to a series of L genes for length of rachis internode.

### *Awning*

Lack of agreement in various reports on the genetics of awning probably arises out of the use of different classifications and material similar in phenotype but differing in genotype.

Tip-awned and fully awned varieties have been found to differ by one gene, with the fully awned condition recessive (38, 62, 4, 21, 20, 32, 67, 66, 46). Segregation appeared to be more complex in crosses involving completely awnless plants. In most cases (13, 4, 14, 11, 45) at least two gene pairs were involved with awn suppression dominant, though in one study (28) the results obtained were attributed to the operation of multiple genes. The most complete study by conventional genetic methods is that of Watkins and Ellerton (69). They postulated that if any two or all three of the genes $B_2$, $B_1$, or $A_3$ were in the homozygous dominant state, the plant would be awnless; if only one were homozygous dominant the plant would be tip-awned, while when all three were homozygous recessive the plant would be fully awned.

### *Spring vs. Winter Habit of Growth*

Most workers have found spring habit of growth dominant, and simple ratios usually have been attained (16, 2, 61, 46). However, Powers (44) concluded that three pairs of genes of unequal effect controlled habit of growth and earliness. Aamodt (1), and Gaines and Singleton (20) found spring habit of growth dominant, but concluded that multiple genes were involved. Hayes and Aamodt (22), while attempting no factorial interpretation, found spring habit of growth and lack of winter hardiness dominant in crosses of Marquis with Minturki and Minhardi.

*Reaction to Leaf Rust*

Wells and Swenson (70) found a single partially dominant gene to be responsible for the resistance of $H_{44}$-Baringa. In a cross between two susceptible varieties, Swenson *et al.* (66) obtained a 9:7 ratio of resistant to susceptible plants in $F_2$. Maines *et al.* (35) concluded that one dominant gene pair was responsible for resistance of Malakoff under greenhouse conditions, while the field resistance of Kanred was dependent on several pairs of genes. In material involving $H_{44}$ as one parent, Hayes *et al.* concluded that one or two pairs of genes were operating.

*Reaction to Bunt*

The resistance of the Martin gene to race T-1 has been found to be dominant by Briggs (9); but Smith (58) has found that the reaction varied depending on what race of the organism was used. Rodenhiser and Holton (47), and Holton (24) have studied and reported the reaction of a large number of varieties when infected with different races of the disease organism. A very complete review of the literature on the genetics of bunt has been published by Holton and Heald (25). Reference will be made later to specific related studies.

## MATERIAL AND METHOD OF PROCEDURE

### Description of Parent Varieties

Two varieties of *Triticum aestivum* L.*, Chinese Spring and Federation 41, and one of *T. compactum* Host., were used in this study. Chinese Spring, a variety of common wheat, was the source of the 17 nulli- or monosomic lines. These lines were obtained from E. R. Sears, and his system of numbering the deficiencies is used throughout the study.

Below is given a description of the varieties with respect to the characters which were studied:

| Character | Variety | | |
|---|---|---|---|
| | Chinese Spring *T. aestivum* | Federation 41 *T. aestivum* | Hymar *T. compactum* |
| Glume colour | White | Red | White |
| Habit of growth | Spring | Spring | Winter |
| Awning | Awnless | Awnless | Short awnlets |
| Reaction to leaf rust, *Puccinia rubigo-vera tritici* Eriks. | Mature plant resistance | Susceptible | Susceptible |
| Reaction to bunt *Tilletia caries* (D.C.) Tul., Race T-16 | Susceptible | Resistant (Martin gene present) | Resistant (Martin gene present) |
| Spike density | Lax | Lax | Dense |

* Synonymous with *T. vulgare* Vill., until recently the commonly accepted botanical name of the species, although *T. aestivum* has priority since it was the original Linnean designation.

**Experimental Methods**

Seed of the 17 different deficient lines was planted in the spring of 1945.

In lines I and VII, nullisomic plants were used as female parents for making the crosses. In two other lines, IX and XVIII, where monosomic plants could be distinguished from normal 2n plants, only monosomics were used. In the other lines, phenotypically normal (in most cases monosomic)* plants were used. Seed was harvested from all parent plants for progeny tests.

Because abnormal transmission of a gene carried by a particular chromosome will occur in $F_2$ families only if the $F_1$ plants are monosomic, it was necessary to determine the chromosomal constitution of the female parent plants in the 13 lines where monosomics were indistinguishable from the disomic plants. This information was obtained by: (1) progeny tests of parent plants to determine if nullisomics were present; (2) cytological observations on the parent plants; (3) cytological observation on $F_2$ families (made on all families of crosses with Federation 41). This latter study also made it possible to infer the chromosomal constitution of the $F_1$ plants.

Since in most cases the same plants were used as female parents for crosses with Federation 41 and Hymar, the results of cytological studies and progeny tests could also be applied to the Hymar crosses.

Glume colour was studied in $F_2$ and $F_3$ populations of the crosses of Federation 41 on the 17 deficient lines of Chinese Spring. The $F_2$ plants were classified as being red- or white-glumed; the $F_3$ lines as homozygous red-glumed, segregating for glume colour, or homozygous white-glumed. Cytological data were obtained on a number of $F_3$ lines and plants grown from abnormally segregating $F_2$ families.

$F_2$ and $F_3$ data on the genetics of spike density were obtained from the crosses of the 17 monosomic (or nullisomic) lines of Chinese Spring with Hymar. In classifying $F_2$ plants, three classes were used: (1) dense, when the spikes were as dense as or denser than spikes of Hymar; (2) lax, when the spikes were as lax as or laxer than spikes of Chinese Spring, and (3) intermediate, when the spikes were intermediate in density. $F_3$ lines were classified as dense, lax, or segregating. Cytological data were obtained on a number of $F_3$ plants grown from $F_2$ plants of abnormally segregating families.

Awning was studied in $F_2$ populations of the crosses of Hymar on the 17 different deficient lines of Chinese Spring. Four classes, depending on the extent of awn development, were used: (1) awnless; (2) awnletted, if short awnlets were present; (3) apically awned, if awns were present on the apex of the spikes, and (4) awned, when the plant was fully awned.

Habit of growth was studied in spring-planted $F_2$ and $F_3$ populations of the crosses of Hymar on the 17 deficient lines of Chinese Spring. At maturity of the spring segregates, $F_2$ plants (or plants in segregating $F_3$ lines) were classified as spring if they were headed, while those that had

* About 75-85 per cent of the functional eggs from monosomic plants are n-1; hence most of the $F_1$ plants from monosomic female parent plants are monosomic (cf. Review of Literature).

failed to show any evidence of jointing were classified as having winter habit of growth. $F_3$ lines were classified as having spring, segregating, or winter habit of growth.

Reaction to leaf rust was studied in crosses of Federation 41 on the 17 different deficient lines of Chinese Spring. $F_2$ data were obtained from special rust nurseries in 1947 and 1948. $F_3$ data also were obtained in 1948. In 1947 $F_2$ plants were classified as resistant, intermediate, or susceptible. In 1948 there was no distinguishable intermediate $F_2$ class. $F_3$ lines were classified as resistant, segregating, or susceptible.

Bunt reaction was studied in $F_2$ populations of crosses of the 17 Chinese Spring deficiencies with both Hymar and Federation 41. From each $F_1$ plant 100 to 150 seeds were inoculated with spores of race T-16* and space planted in a nursery at the Pendleton Field Station, Pendleton, Oregon, in the fall of 1946. A similar nursery from the crosses involving Federation 41 was planted at Pullman in the spring of 1947. Where $F_3$ data were needed, seeds from smut-free $F_2$ plants were inoculated and tested in the same way. At maturity $F_2$ plants were examined for smutted spikes and classified into four classes with respect to the presence of smut: (1) all spikes smutted; (2) most spikes of main tillers smutted; (3) few spikes smutted. and (4) smut-free. $F_3$ lines were classified as smut-free or segregating. For analysis of the data classes 1 and 2 were combined into the susceptible class, and classes 3 and 4 into the resistant class. For computing Chi-square, the data were corrected for escapes of the susceptible genotypes, The percentage of escapes of Chinese Spring was used as the basis for correction.

Cytological observations were made using the acetocarmine and acetoorcein smear techniques which have been described in greater detail by Smith (57). Whole spikes of the parent plants were collected in 1945, fixed in Carnoy's fluid for three to four days, and stored in 70 per cent alcohol at 5° to 10° C. until the summer of 1948. Spikes of $F_2$ plants were collected in the summer of 1947. They were fixed and stored in Carnoy's fluid until they were examined in 1948. Spikes of $F_3$ plants were fixed in Carnoy's fluid for three to four days, after which they were studied cytologically. Root-tips were pre-treated in a saturated solution of paradichlorobenzene for from five to six hours, fixed in Farmers' fluid for from two to three days, and stored in 70 per cent alcohol until used.

Observations on pollen mother cells were made on acetocarmine smear preparations. In most cases chromosome counts could be made at a magnification of about 400 diameters using a 40x high dry objective and a 10x ocular. In some cases, where meiosis had been completed and where it was necessary only to determine whether or not a plant was monosomic, the presence of micronuclei in a high percentage of the quartets was taken as evidence that the plant was monosomic. In most cases, however, actual counts of chromosomes were obtained. Root-tip examinations were on acetoorcein smear preparations.

Photomicrographs of microsporocytes were taken of acetocarmine smear slides made permanent by the tertiary-butyl alcohol method. Photomicrographs of root-tip cells were taken of freshly prepared slides.

* Inoculum kindly supplied by C. S. Holton.

TABLE 1.—CHROMOSOMAL CONSTITUTION OF FEMALE PARENTS AND $F_1$'S OF MONOSOMIC (OR CORRESPONDING NULLISOMIC) LINES OF CHINESE SPRING × FEDERATION 41

| Chromosome tested | Constitution of parents as indicated by: Phenotype | Progeny test | Cytologic observation | $F_1$ plants tested | Constitution of $F_2$ plants: $21^{II}$ | $20^{II}1^{I}$ | $20^{II}$ | Total | Constitution of $F_1$ plants (inferred): $20^{II}1^{I}$ | $21^{II}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | No. | No. | No. | No. | No. | No. | No. |
| I | 2n-2 | 2n-2 | — | 6 | 3 | 12 | — | 15 | 6* | 0 |
| II | ? | — | $20^{II}1^{I}$ | — | — | — | — | — | — | — |
| | ? | 2n-1 | — | 3 | 4 | 3 | 0 | 7 | 2 | 1 |
| | ? | 2n-1 | — | 3 | 2 | 6 | 0 | 8 | 3 | 0 |
| III | ? | 2n-1 | $20^{II}1^{I}$ | 3 | 5 | 5 | 0 | 10 | 2 | 1 |
| | ? | 2n-1 | $20^{II}1^{I}$ | 3 | 0 | 6 | 0 | 6 | 3 | 0 |
| IV | ? | ? | $20^{II}1^{I}$ | 6 | 5 | 9 | 0 | 14 | 5 | 1 |
| V | ? | 2n-1 | $20^{II}1^{I}$ | — | — | — | — | — | — | — |
| | ? | 2n-1 | — | 3 | 1 | 5 | 0 | 6 | 3 | 0 |
| | ? | 2n-1 | $20^{II}1^{I}$ | 3 | 4 | 4 | 0 | 8 | 2 | 1 |
| VI | ? | 2n-1 | $20^{II}1^{I}$ | 6 | 7 | 8 | 0 | 15 | 5 | 1 |
| | ? | 2n | $20^{II}1^{I}$ | — | — | — | — | — | — | — |
| | ? | 2n | $20^{II}1^{I}$ | — | — | — | — | — | — | — |
| VII | 2n-2 | 2n-2 | $20^{II}$ | 6 | 3 | 16 | 0 | 19 | 6 | 0 |
| VIII | ? | 2n-1 | — | 3 | 6 | 6 | 0 | 12 | 2 | 1 |
| | ? | 2n-1 | $20^{II}1^{I}$ | 2 | 4 | 4 | 0 | 8 | 1 | 1 |
| IX | 2n-1 | 2n-1 | $20^{II}1^{I}$ | 3 | 0 | 5 | 0 | 5 | 3 | 0 |
| | 2n-1 | 2n | $20^{II}1^{I}$ | — | — | — | — | — | — | — |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| X | ? | 2n | — | 3 | 6 | 2 | 0 | 8 | 2 | 1 |
| | ? | 2n | $20^{II}1^{I}$ | 3 | 4 | 3 | 0 | 7 | 2 | 1 |
| XI | ? | 2n | $20^{II}1^{I}$ | 3 | 3 | 6 | 0 | 9 | 3 | 0 |
| | ? | 2n | — | 3 | 10 | 2 | 0 | 12 | 1 | 2 |
| XV | ? | 2n-1 | $20^{II}1^{I}$ | 3 | 0 | 7 | 0 | 7 | 3 | 0 |
| | ? | 2n-1 | $20^{II}1^{I}$ | 3 | 1 | 6 | 0 | 7 | 3 | 0 |
| | ? | 2n | $21^{II}$ | — | — | — | — | — | — | — |
| XVI | ? | 2n-1 | — | 3 | 1 | 4 | 0 | 5 | 3 | 0 |
| | ? | 2n-1 | $20^{II}1^{I}$ | 3 | 5 | 4 | 0 | 9 | 2 | 1 |
| XVII | ? | 2n | — | 3 | 5 | 3 | 0 | 8 | 2 | 1 |
| | ? | 2n | — | 3 | 8 | 3 | 1 | 12 | 1 | 2 |
| | ? | 2n | — | 3 | 5 | 2 | 2 | 9 | 2 | 1 |
| XVIII | 2n-1 | 2n-1 | $20^{II}1^{I}$ | 6 | 6 | 12 | 0 | 18 | 5 | 1 |
| XIX | ? | 2n-1 | $20^{II}1^{I}$ | 6 | 5 | 19 | 0 | 24 | 5 | 1 |
| XX | ? | 2n-1 | $20^{II}1^{I}$ | 3 | 4 | 5 | 0 | 9 | 2 | 1 |

* If the first plant in an $F_2$ family was found to be monosomic, usually no more plants were examined.

## EXPERIMENTAL RESULTS

### Chromosomal Constitution of Female Parents and of $F_1$'s from Monosomic (or Corresponding Nullisomic) Lines of Chinese Spring × Federation 41

The results of progeny tests and cytological studies of the female parent plants, as well as determinations of the chromosomal constitution of the $F_1$'s from cytological studies on $F_2$ plants are presented in Table 1.

In 10 cases the chromosomal constitution of the female parent plants was not shown by the progeny test. This may be explained on the basis of: (1) small populations; (2) low transmission of n-1 male gametes, or (3) low survival of nullisomic plants. In the case of all 17 lines tested, however, at least some of the $F_1$ plants were monosomic as shown by cytological studies on $F_2$ plants. Thus, data on the effect of each of the 17 chromosome deficiencies on the transmission of the genes for the several characters were obtained.

### Chromosomal Constitution of Female Parents and of $F_1$'s from Monosomic (or Corresponding Nullisomic) Lines of Chinese Spring × Hymar

As indicated earlier, the female parent plants used for making these crosses, in most cases, were the same as those used in the Federation 41 crosses. It is assumed, therefore, that in these crosses the $F_2$ families representing the 17 different chromosome deficiencies also were from monosomic $F_1$ plants.

*Glume Colour*

The data on segregation of glume colour in $F_2$ and $F_3$ populations from crosses of Federation 41 on the 17 different monosomic (or corresponding nullisomic) lines of Chinese Spring are summarized in Table 2.

Excepting for families involving chromosome I, the $F_2$ results clearly indicate that a single dominant gene pair was responsible for red glumes in Federation 41. These results are substantiated by the close fit to a 1 : 2 : 1 ratio of homozygous red-glumed : segregating : homozygous white-glumed lines in the 139 $F_3$ lines tested.

The unsatisfactory fit obtained when the results of all $F_2$ families, excluding those involving chromosome I, are combined probably can be attributed to errors in classification of some white-glumed plants. Since these same populations were used for studying bunt reaction and since smut causes glume discoloration, it is likely that some genetically white-glumed plants were classified as having red glumes. This error would be consistent and the deviation would be cumulative, resulting in a highly significant $X^2$ when the data are combined.

Segregation for glume colour in the chromosome I families was obviously different from that in other families. The proportion of white-glumed plants was abnormally low, and judged by their lack of vigour and fertility, all of these white-glumed plants were nullisomic. This indicates conclusively that the gene for red glumes of Federation 41 is carried by chromosome I.

In Figure 1, spikes from red- and white-glumed (presumably nullisomic) $F_2$ plants of families involving chromosome I are illustrated.

TABLE 2.—SEGREGATION FOR GLUME COLOUR IN $F_2$ AND $F_3$ POPULATIONS FROM CROSSES OF FEDERATION 41 ON THE 17 DIFFERENT MONOSOMIC (OR CORRESPONDING NULLISOMIC) LINES OF CHINESE SPRING

| Chromosome tested | Red-glumed | Segregating | White-glumed | Total | $X^2$ for ratio of 3 : 1 in $F_2$ and 1 : 2 : 1 in $F_3$ |
|---|---|---|---|---|---|
| | No. | No. | No. | No. | |
| I | 528 | — | 38 | 566 | 100.93** |
| II | 637 | — | 193 | 830 | 1.35 |
| III | 628 | — | 219 | 847 | 0.33 |
| IV | 600 | — | 196 | 796 | 0.06 |
| V | 652 | — | 202 | 854 | 0.83 |
| VI | 748 | — | 228 | 976 | 1.45 |
| VII | 659 | — | 208 | 867 | 0.47 |
| VIII | 690 | — | 213 | 903 | 0.96 |
| IX | 248 | — | 73 | 321 | 0.87 |
| X | 797 | — | 248 | 1045 | 0.89 |
| XI | 915 | — | 292 | 1207 | 0.42 |
| XV | 708 | — | 224 | 932 | 0.47 |
| XVI | 814 | — | 264 | 1078 | 0.15 |
| XVII | 1308 | — | 417 | 1725 | 0.63 |
| XVIII | 578 | — | 174 | 752 | 1.39 |
| XIX | 679 | — | 212 | 891 | 0.69 |
| XX | 314 | — | 99 | 413 | 0.23 |
| Total (excluding families involving chromosome I) | 10,975 | — | 3,462 | 14,437 | 8.00** |
| $F_3$ lines* | 33 | 70 | 36 | 139 | 0.12 |

* The $F_3$ data on normal segregation were obtained from families segregating monosome XVI, but could have been obtained from any $F_3$ families other than those segregating monosome I.
** Significant at the 1 per cent level.

Because the $F_2$ results had indicated that the gene for red glume colour was carried by chromosome I, an effort was made to correlate genetic with cytologic observations. Microsporogenesis was studied in plants of a number of $F_3$ families grown from red- and white-glumed $F_2$ plants in families involving chromosome I. At maturity, the glume colour of plants studied cytologically was recorded. These data are summarized in Table 3.

TABLE 3.—CHROMOSOMAL CONSTITUTION AND GLUME COLOUR OF $F_3$ PLANTS FROM RED- AND WHITE-GLUMED $F_2$ PLANTS OF THE CROSS NULLISOMIC I × FEDERATION 41

| $F_2$ parent plants | | | $F_3$ plants | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Glume colour | Chromosome* constitution | Total studied | $21^{II}$ | | $20^{II}1^{I}$ | | $20^{II}$ | | Total $F_3$ plants studied |
| | | | Red | White | Red | White | Red | White | |
| | | No. | No. | No. | No. | No. | No. | No. | No. |
| Red | 2n | 14 | 53 | 0 | 0 | 0 | 0 | 0 | 53 |
| Red | 2n-1 | 10 | 18 | 0 | 119 | 0 | 0 | 0 | 137 |
| White | 2n-2 | 6 | 0 | 0 | 26 | 11 | 0 | 0 | 37 |
| Total | | 30 | 71 | 0 | 145 | 11 | 0 | 0 | 227 |

* Inferred from observations on $F_3$ plants.

As expected, no white-glumed 2n or 2n-1 $F_3$ plants were present in the progenies of red-glumed $F_2$ plants. It was surprising, however, that not a single 2n-2 plant was found in any of the families that segregated monosomics. This may have been because there was a severe infestation of the wheat stem maggot* in the nursery. Nullisomics, being weak and producing few culms even under ideal conditions, were possibly unable to survive attack by the parasites.

There was no apparent difference in glume colour of disomic and monosomic $F_3$ plants. Thus, one gene was adequate for developing full red glume colour. In Figure 2 a microsporocyte and a spike from a monosomic $F_3$ plant are illustrated.

The $F_3$ results from white-glumed (presumably nullisomic) $F_2$ plants require some explanation. Obviously selfed progeny from them should be like the parents, i.e., white-glumed and nullisomic. The $F_2$ plants were allowed to open-pollinate, and consequently a high percentage (or possibly all) of their progeny resulted from natural crosses, since nullisomic I plants are almost completely male sterile. At any rate, the 26 red-glumed $F_3$ monosomic plants must have resulted from natural crossing.

The assumption that the white-glumed $F_2$ plants were nullisomic and cross pollinated is further supported by the fact that all progenies examined cytologically were 2n-1.

*Spike Density*

The data on segregation of spike types in $F_2$ and $F_3$ populations of the crosses of Hymar on the 17 different monosomic (or corresponding nullisomic) lines of Chinese Spring are summarized in Table 4.

In $F_2$ families of chromosomes not associated with the gene conditioning spike density, a simple monohybrid ratio was expected. However, the expected ratios were not obtained, probably because of erroneous classification of a number of $F_2$ plants. The same families were used also in the study of bunt reaction, and probably some smutted plants were wrongly classified, since the diseased spikes were abnormally elongated.

Segregation in $F_2$ populations indicated that a single gene pair was mainly responsible for differentiation between the true lax and the true dense spike types. However, there was evidence of transgressive segregation, some plants having spikes more dense than Hymar, and others having spikes more lax than Chinese Spring (Figure 3). This indicated that there were other (possibly only modifying) genes which affected density of spikes.

Segregation in $F_2$ families involving chromosome XX was distinctly different from that in families in which the other 16 chromosomes were tested. There were only 11 lax-spiked $F_2$ plants. The lack of vigour and the low fertility of these plants indicated that they were probably nullisomic (Figure 4A). These results suggested that the main gene for dense spikes in Hymar was carried by chromosome XX.

$F_3$ data obtained from 112 $F_2$ plants were not entirely as expected. In 29 of the $F_3$ progenies there were 51 lax-spiked plants; 10 of the 51 were similar to the 11 presumably nullisomic $F_2$ plants, the remaining 41 plants had normal vigour and fertility, and at maturity 19 of the 41 were found

* Larvae of the insect were present in approximately half of the plants examined cytologically.


Figure 1. (*left*) A. Spikes from white-glumed, apparently Nullisomic I, $F_2$ plants.
B. Spikes from red-glumed, normal or monosomic I, $F_2$ plants.

Figure 2. (*lower left*) A. A microsporocyte from a 2n-1 $F_3$ plant of nullisomic I × Federation 41. There are 13 closed pairs, seven open pairs, one univalent (arrow).

B. A spike from the same plant as Figure 2A. The glumes were red and indistinguishable from 2n plants.

Figure 3. (*lower right*) Spike and rachis types of parents, and segregates from crosses of Hymar on the 17 different deficient lines of Chinese Spring.

A. Hymar.

B. and C. $F_3$ segregates.

D. Chinese Spring.

Fig. 2

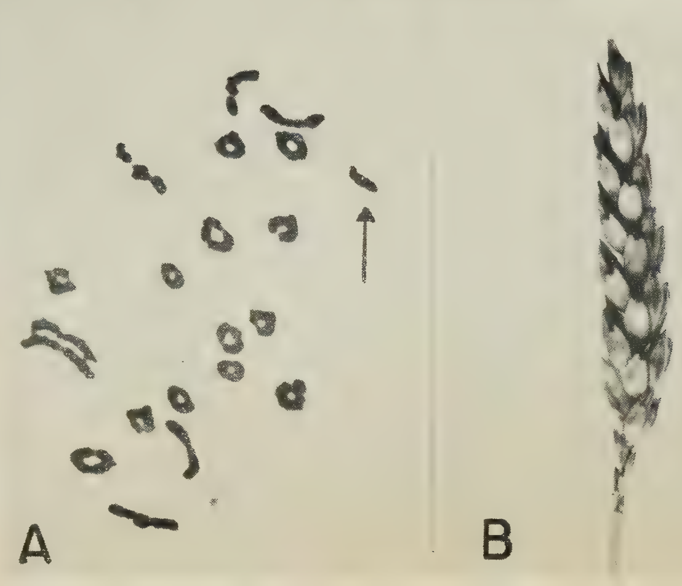



Fig. 3


FIGURE 5. Awn types of parent and $F_2$ plants of the crosses of Hymar on the 17 different monosomic (or corresponding nullisomic) lines of Chinese Spring.

A. Spikes from fully awned $F_2$ plants.

B. Spikes from apically awned $F_2$ plants.

C. Spikes from awnletted $F_2$ plants.

D. Spikes from awnless $F_2$ plants.

E. Spike from Chinese Spring.

F. Spike from Hymar.


FIGURE 4. Spikes from $F_2$ plants of the cross of Hymar on Chinese Spring deficient for chromosome XX.

A. Spike from plant presumed to have 2n-2 chromosomes.

B. Spikes from plants presumed to have 2n or 2n-1 chromosomes.


FIGURE 6. Spikes from $F_2$ plants of the cross of Hymar × monosomic IX of Chinese Spring.

A. and B. Spikes from monosomic (heterozygous speltoid) plants.

C. Spike from a plant that was presumably nullisomic (homozygous speltoid).

TABLE 4.—SEGREGATION OF SPIKE TYPES IN $F_2$ AND $F_3$ POPULATIONS OF THE CROSSES OF HYMAR ON THE 17 MONOSOMIC (OR CORRESPONDING NULLISOMIC) LINES OF CHINESE SPRING

| Chromosome tested | Spike type of plants (lines in $F_3$): Dense | Intermediate (or segregating in $F_3$) | Lax | Total | $X^2$ for 1 : 2 : 1 ratio |
|---|---|---|---|---|---|
| | No. | No. | No. | No. | |
| I | 57 | 98 | 78 | 233 | —* |
| II | 143 | 125 | 119 | 387 | — |
| III | 117 | 113 | 87 | 317 | — |
| IV | 62 | 67 | 53 | 182 | — |
| V | 119 | 97 | 95 | 311 | — |
| VI | 90 | 85 | 89 | 264 | — |
| VII | 60 | 54 | 47 | 161 | — |
| VIII | 174 | 175 | 157 | 506 | — |
| IX | 96 | 140 | 142 | 378 | — |
| X | 166 | 199 | 158 | 543 | — |
| XI | 195 | 187 | 149 | 531 | — |
| XV | 104 | 112 | 88 | 304 | — |
| XVI | 134 | 108 | 102 | 344 | — |
| XVII | 107 | 91 | 91 | 289 | — |
| XVIII | 141 | 139 | 122 | 402 | — |
| XIX | 35 | 52 | 47 | 134 | — |
| XX | 154 | 66 | 11 | 231 | — |
| Total (excluding families involving chromosome XX) | 1820 | 1842 | 1624 | 5286 | — |
| $F_3$ lines** | 124 | 249 | 118 | 491 | 0.24 |

* The $F_2$ data could not be fitted to a 1 : 2 : 1 ratio, so $X^2$ was not computed.

** These data on normal segregation were obtained from families segregating monosomes IX and X, but could have been obtained from any families other than those segregating monosome XX. Since the segregation in families involving the monosomes IX and X was similar, the data are combined.

to be red-glumed. This suggests that probably all 41 lax-spiked plants with normal vigour were natural crosses; certainly the red-glumed ones were, since Hymar and Chinese Spring both have white glumes.

The cytological data on $F_3$ lines obtained from $F_2$ populations involving chromosome XX are summarized in Table 5.

While no nullisomic plants were found among the 71 plants studied, a high proportion of the plants had aberrations other than univalents. These aberrations involved chains of three or four chromosomes, heteromorphic bivalents, pairs of telocentric chromosomes and isochromosomes. All plants with the normal chromosomal complement had dense spikes, while those with 20 pairs of chromosomes plus one univalent or 20 pairs plus one heteromorphic bivalent, had spikes of intermediate density. The fact that plants with 20 pairs plus one heteromorphic bivalent had spikes of intermediate density indicates that the Hymar gene for spike density was not present in the telocentric chromosome. It can further be inferred that the telocentric chromosome was present in the plant used as the female parent in making the crosses, since the aberration was present in $F_3$ lines obtained from four different $F_2$ families.

It is likely that the chains of three or four chromosomes were the result of supernumerary chromosomes rather than reciprocal translocations. The one plant with a chain of four chromosomes (cf. Table 5) had in addition

Table 5.—Chromosomal constitution and spike type of $F_3$ plants of the cross of Hymar on a line of Chinese Spring which was deficient for chromosome XX

| Total chromosomes* | Chromosomal constitution | Spike type | $F_3$ plants studied | $F_3$ families represented |
|---|---|---|---|---|
| No. | | | No. | No. |
| 42 | $21^{II}$ | Dense | 21 | 10 |
| 41 | $20^{II}1^{I}$ | Intermediate | 13 | 5 |
| 42 | $20^{II}1^{I}$ heteromorph. pr. | Intermediate | 23 | 7 |
| 44 | $22^{II}$ | Dense | 1 | 1 |
| 44 | $20^{II}2^{I}$ 1 het. pr. | Lax, normal | 1 | 1 |
| 43 | $19^{II}$ 1 telo. pr. $1^{III}$ | Intermediate | 1 | 1 |
| 44 | $20^{II}$ $1^{IV}$ | (Died) | 1 | 1 |
| 41 | $20^{II}$ 1 iso. | Int. to near lax | 3 | 1 |
| 43 | $19^{II}$ 1 iso. $1^{III}$ | Int. to near lax | 1 | 1 |
| 42 | $19^{II}2^{I}$ 1 het. pr. | Intermediate | 3 | 1 |
| 43 | $20^{II}$ $1^{I}$ 1 het. pr. | Dense | 1 | 1 |
| 44 | $21^{II}$ 1 telo. pr. | Dense | 1 | 1 |
| 43 | $20^{II}1^{I}$ 1 telo. pr. | Dense | 1 | 1 |

* Includes also half chromosomes and isochromosomes.

20 normal pairs of chromosomes. One possible source of plants with such a chromosomal constitution would be plants with two or more univalents, or with chains of three chromosomes (Sears 50, 52).

The cytological studies showed that the $F_2$ and $F_3$ plants with lax spikes, and which were classified as nullisomic, had a pair of telocentric chromosomes (Plate I, I). The root-tip cell illustrated in Plate I, J is from one of the 10 $F_3$ plants that were classified as nullisomic (spike illustrated in Plate II G). This plant had 40 normal and two half (presumably telocentric) chromosomes, and it is probable that this was the chromosomal constitution of all $F_2$ and $F_3$ plants in this family that were classified as nullisomic.

## Plate I

Microsporocyte and root-tip cells from $F_3$ plants of the cross of Hymar on Chinese Spring, deficient for chromosome XX.

A. Microsporocyte from a disomic plant, 21 pairs.

B. Microsporocyte from a monosomic plant, 18 closed pairs, 2 open pairs, 1 univalent (arrow).

C. Microsporocyte from a plant with 18 closed pairs, 1 open pair, 2 univalents (8 and 9 o'clock), 1 heteromorphic bivalent (arrow).

D. Microsporocyte from a plant with 19 closed pairs, 1 disjoined pair, 1 chain of 4 (arrow), 2n = 44.

E. Microsporocyte from the same floret as D, chain of 4 chromosomes (arrow).

F. Microsporocyte showing 1 heteromorphic bivalent at diakinesis (arrow). There also is evidence of a multiple association in the centre of the group.

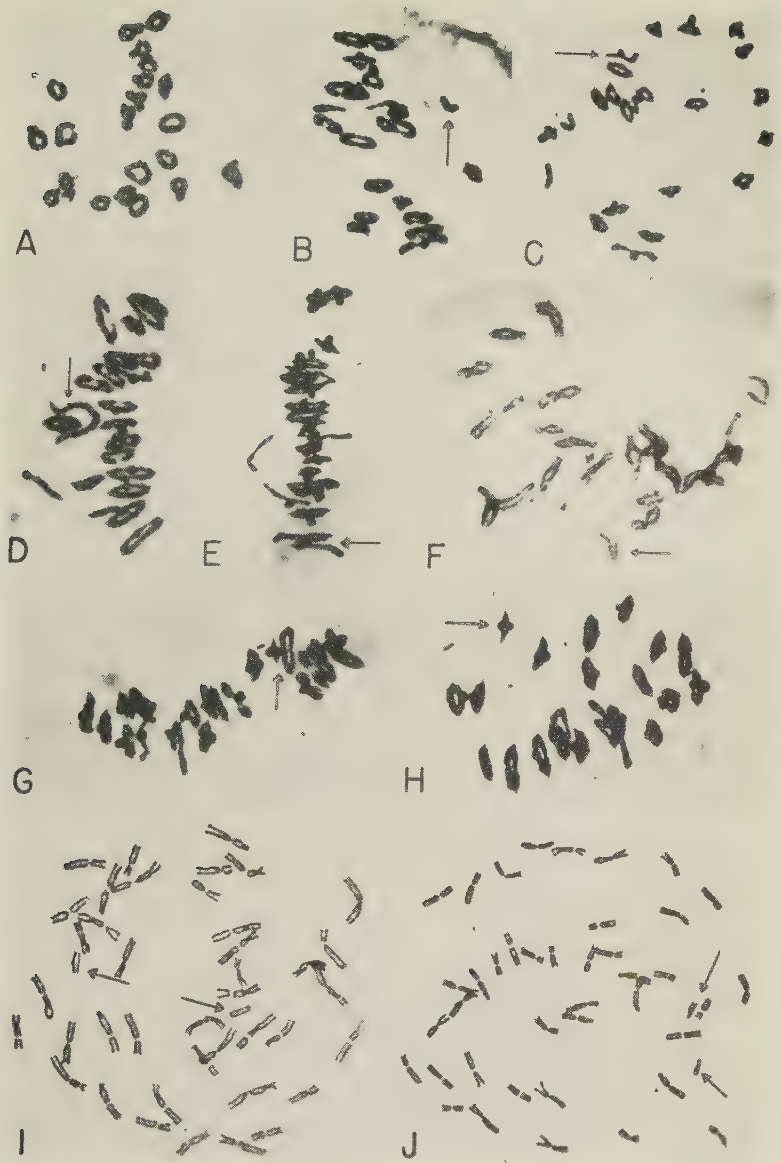
G. Microsporocyte from a plant with 1 (presumably) telocentric chromosome pair (arrow), 18 closed pairs, 1 chain of 3 chromosomes (bottom centre).

H. Microsporocyte from a plant of the same $F_3$ line as G, 20 closed pairs, 1 (presumably) telocentric pair (arrow), 1 open pair.

I. Root-tip metaphase from a progeny of plant G, 40 normal and 2 half (presumably telocentric) chromosomes (arrow).

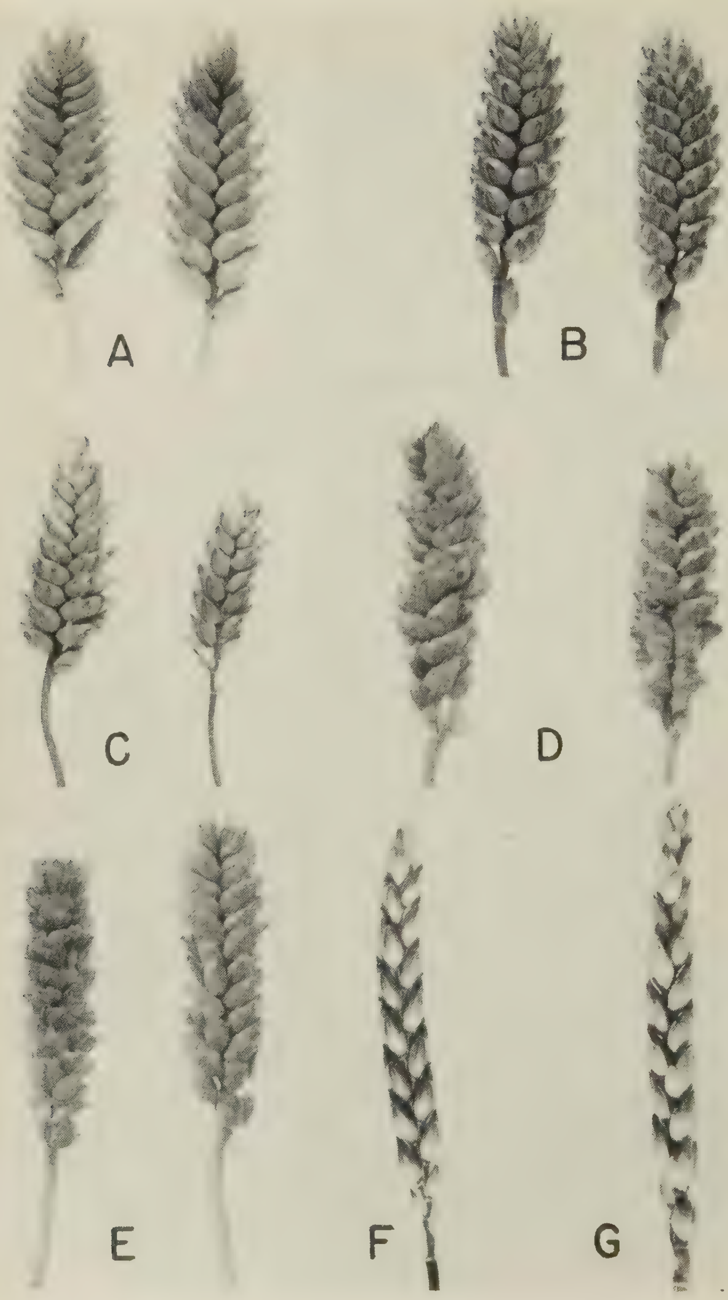
J. Root-tip metaphase from a progeny of an $F_2$ plant presumed to be nullisomic. There appear to be 40 normal chromosomes and 2 half (presumably telocentric) chromosomes (arrow).

(Magnifications of all photomicrographs approximately 1080x).




(Legend on page 78)

PLATE II

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*Awning*

The data on segregation of awn types in $F_2$ families of the crosses of Hymar on the 17 different monosomic (or corresponding nullisomic) lines of Chinese Spring are summarized in Table 6.

TABLE 6.—SEGREGATION OF AWN TYPES IN $F_2$ POPULATIONS FROM CROSSES OF HYMAR ON THE 17 DIFFERENT MONOSOMIC (OR CORRESPONDING NULLISOMIC) LINES OF CHINESE SPRING

| Chromosome tested | Awnless and awnletted | Apically awned and awned | Total | $X^2$ for ratio of 57 : 7 |
|---|---|---|---|---|
| | No. | No. | No. | |
| I | 26 | 2 | 28 | 0.35 |
| II | 159 | 16 | 175 | 0.56 |
| III | 51 | 11 | 62 | 2.98 |
| IV | 57 | 11 | 68 | 1.96 |
| V | 61 | 7 | 68 | 0.04 |
| VI | 83 | 10 | 93 | <0.01 |
| VII | 31 | 4 | 35 | <0.01 |
| VIII | 227 | 56 | 283 | 23.76* |
| IX | 137 | 0 | 137 | 16.84* |
| X | 181 | 40 | 221 | 11.68* |
| XI | 215 | 23 | 238 | 0.39 |
| XV | 148 | 19 | 167 | <0.01 |
| XVI | 151 | 18 | 169 | <0.01 |
| XVII | 158 | 15 | 173 | 0.89 |
| XVIII | 152 | 13 | 165 | 1.56 |
| XIX | 95 | 11 | 106 | 0.01 |
| XX | 177 | 13 | 190 | 3.28 |
| Total $F_2$ (excluding families involving chromosomes VIII, IX, and X). | 1564 | 173 | 1737 | 1.70 |

* Significant at the 1 per cent level.

Although Chinese Spring is awnless, and Hymar has only very short awnlets, fully awned, awnless and various intermediate types were observed in $F_2$ populations, as illustrated in Figure 5. According to Sears (50), Chinese Spring has one dominant awn inhibiting gene in chromosome VIII and another in chromosome X. Evidently Hymar had the recessive alleles in these same chromosomes, but also a dominant awn-inhibiting gene in a

PLATE II

Spikes from cytologically examined $F_3$ plants of the cross of Hymar on Chinese Spring, deficient for chromosome XX.

A. Spike from a 2n plant classified as dense.

B. Spike from a 2n-1 plant classified as intermediate.

C. Spike from a plant with 1 chain of 4 and 20 pairs of chromosomes.

D. Spike from a plant with 1 heteromorphic bivalent (from same plant as microsporocyte in Plate I, F).

E. Spike from a plant with 41 normal chromosomes and 1 (presumably) telocentric pair (from same plant as microsporocyte in Plate I, G).

F. Spike from a plant with 40 normal and 2 half (presumably) telocentric chromosomes. This plant was from progeny of the plant illustrated in Plate II, E.

G. Spike from a plant classified as nullisomic. (Microsporocyte from a progeny of this plant illustrated in Plate I, J)

(Magnification approximately 1x).

chromosome other than VIII and X. Consequently, a trihybrid ratio would be expected in the $F_1$ families involving chromosomes not associated with genes for awns. If the awnless and awnletted plants are combined into one class and apically awned and fully awned plants also are grouped, and further, if it is assumed that plants with two or more dominant awn inhibitor genes were awnless or awnletted, the expected $F_2$ ratio would be 57 awnless and awnletted : 7 apically awned and awned plants.

With the exception of families involving chromosomes VIII, IX, and X, the results obtained (taken separately or collectively) were in fairly good agreement with the expected ratio, although some of the populations were small. The distribution of awn types was distinctly different in families segregating monosomes VIII, IX, and X from that in families involving the other 14 chromosomes.

In families involving chromosomes VIII and X, there was a much higher proportion of apically-awned and fully awned plants than in families involving the other chromosomes tested. This would be expected if the recessive alleles of the two awn-inhibiting genes of Chinese Spring are carried by chromosomes VIII and X of Hymar. The ratio in families involving these two chromosomes closely approached 50 awnless and awnletted: 14 apically awned and fully awned, the $X^2$ being 0.005 and 0.72 for families involving chromosomes VIII and X, respectively. Such a ratio would result if in families involving these chromosomes, the monosomic plants that were heterozygous for the Hymar awn-inhibiting gene were awnletted. In Table 7 hypothetical genotypes and phenotypes for families involving these two chromosomes are suggested. Since there were

TABLE 7.—POSTULATED $F_2$ PHENOTYPES AND GENOTYPES OF CROSSES OF HYMAR ON MONOSOMIC (OR NULLISOMIC) LINES VIII AND X OF CHINESE SPRING

| Awnless and awnletted classes | | Apically awned and awned classes | |
|---|---|---|---|
| Genotype | Proportion of 64 | Genotype | Proportion of 64 |
| | No. | | No. |
| a a $A_2A_2A_3A_3$* | 1 | a a $A_2a_2a_3a_3$ | 2 |
| – a $A_2A_2A_3A_3$** | 3 | a a $a_2a_2A_3a_3$ | 2 |
| a a $A_2A_2a_3a_3$ | 1 | – a $a_2a_2A_3a_3$ | 6 |
| – a $A_2A_2a_3a_3$ | 3 | a a $a_2a_2a_3a_3$ | 1 |
| a a $A_2a_2A_3A_3$ | 2 | – a $a_2a_2a_3a_3$ | 3 |
| – a $A_2a_2A_3A_3$ | 6 | | |
| a a $A_2a_2A_3a_3$ | 4 | | |
| – a $A_2a_2A_3a_3$ | 12 | | |
| a a $A_2A_2A_3a_3$ | 2 | | |
| – a $A_2A_2A_3a_3$ | 6 | | |
| a a $a_2a_2A_3A_3$ | 1 | | |
| – a $a_2a_2A_3A_3$ | 3 | | |
| – a $A_2a_2a_3a_3$ | 6 | | |
| Total | 50 | | 14 |

* A was suggested as the symbol for genes of awns by the committee on nomenclature and genetic factors in wheat (5). It is here suggested that A without subscript and $A_2$ and $A_3$ be used to denote the awning genes in chromosomes VIII, IX, and X, respectively.

** – Indicates the absence of a gene in monosomic plants. The table suggests genotypes for families segregating monosomic VIII plants. For families where chromosome X was involved the same proportions would be obtained, but $A_3$ would be affected.

only a few nullisomics, they have been omitted entirely. It also was assumed that monosomic and disomic plants were present in a proportion of 75 : 25, respectively (cf. Review of Literature).

The validity of including the – a $A_2a_2a_3a_3$ genotype in the awnless and awnletted class is questionable. This can be justified only if $A_2$, the Hymar awn inhibiting gene, has greater effect than either of the Chinese Spring genes A and $A_3$. Results obtained in families segregating monosomic IX plants indicated that this might be a valid assumption.

Segregation for awns in families involving the chromosome IX deficient line of Chinese Spring was distinctly different from that in families involving all the other chromosomes. At the most, disomic and monosomic plants were awnletted, and only the occasional nullisomic plant had appreciable awn development (Figure 6). This indicates that the dominant awn inhibiting gene of Hymar was carried by chromosome IX. The fact that none of the monosomic plants (easily identified since they were speltoid) was apically-awned is evidence of the correctness of the conclusion reached earlier; namely, that the Hymar gene has greater effect on inhibiting awn development than either of the two genes in Chinese Spring.

*Spring vs. Winter Habit of Growth*

The data on segregation for growth habit in $F_2$ and $F_3$ populations from the crosses of Hymar on the 17 deficient lines of Chinese Spring are summarized in Table 8.

The $F_2$ results, with the exception of those from chromosome IX families, closely fit a ratio of 15 spring: 1 winter, indicating that duplicate genes conditioned habit of growth in these crosses. While a significant $X^2$ was obtained in chromosome I and chromosome XX families, the results were close to the expected 15 : 1 ratio. The combined data also showed a very good fit to the duplicate gene $F_2$ ratio. Finally, this hypothesis was satisfactorily corroborated by the data from $F_3$ lines where a good fit to the expected ratio of 7 homozygous spring: 8 segregating: 1 homozygous winter line was obtained.

Segregation in $F_2$ and $F_3$ populations of chromosome IX was distinctly different from that observed in the other families. Actually, the data from $F_2$ populations combined with those from segregating $F_3$ lines involving chromosome IX give a very good fit to a 3 : 1 ratio. If one of the duplicate genes was carried by chromosome IX, this would be the ratio expected, since only the 1 dominant gene for spring growth habit of Chinese Spring (not carried by chromosome IX) would be segregating in these families. $F_3$ lines obtained from spring planted $F_2$ progenies would consist of one spring: two segregating, which was approximately the ratio obtained. There would be no true-breeding winter $F_3$ lines since no $F_2$ plants with the genotype for winter growth habit would have produced seed.

These results, therefore, clearly show that one of the duplicate genes conditioning habit of growth in these crosses was carried by chromosome IX.

*Reaction of Leaf Rust*

The data on leaf rust reaction of $F_2$ plants and $F_3$ lines from the crosses of Federation 41 on the 17 different monosomic (or corresponding nullisomic) lines of Chinese Spring are summarized in Table 9.

TABLE 8.—SEGREGATION FOR GROWTH HABIT IN $F_2$ AND $F_3$ POPULATIONS FROM THE CROSSES OF HYMAR ON THE 17 DIFFERENT MONOSOMIC (OR CORRESPONDING NULLISOMIC) LINES OF CHINESE SPRING

| Chromosome tested | Growth habit of plants or lines | | | Total | Ratio expected | $X^2$ |
|---|---|---|---|---|---|---|
| | Spring | Segregating | Winter | | | |
| I | 432 | — | 16 | 448 | 15 : 1 | 5.48† |
| II | 538 | — | 36 | 574 | 15 : 1 | 0.01 |
| III | 591 | — | 36 | 637 | 15 : 1 | 0.28 |
| IV | 236 | — | 18 | 254 | 15 : 1 | 0.33 |
| V | 499 | — | 29 | 528 | 15 : 1 | 0.51 |
| VI | 520 | — | 35 | 555 | 15 : 1 | 0.03 |
| VII | 290 | — | 12 | 302 | 15 : 1 | 2.63 |
| VIII | 457 | — | 33 | 490 | 15 : 1 | 0.20 |
| IX* | 3416 | — | 1107 | 4522 | 15 : 1 | Very large†† |
| IX** | 365 | — | 28 | 393 | 15 : 1 | 0.51 |
| X | 944 | — | 68 | 1012 | 15 : 1 | 0.38 |
| XI | 716 | — | 44 | 760 | 15 : 1 | 0.28 |
| XV | 461 | — | 37 | 498 | 15 : 1 | 1.18 |
| XVI | 571 | — | 38 | 609 | 15 : 1 | 0.01 |
| XVII | 342 | — | 18 | 360 | 15 : 1 | 0.96 |
| XVIII | 784 | — | 49 | 833 | 15 : 1 | 0.19 |
| XIX | 42 | — | 5 | 47 | 15 : 1 | 1.51 |
| XX | 52 | — | 8 | 60 | 15 : 1 | 5.14† |
| Total $F_2$ (excluding families involving chromosome IX) | 7840 | — | 510 | 8350 | 15 : 1 | 0.29 |
| $F_3$ lines*** | 51 | 54 | 7 | 112 | 7 : 8 : 1 | 0.15 |
| IX $F_3$ lines | 93 | 144 | 0 | 237 | 1 : 2 | 3.72 |

* Combined data from $F_2$ populations and from segregating $F_3$ lines.
** $F_2$ data from disomic $F_1$'s.
*** The $F_3$ data on normal segregation were obtained from fall-planted families segregating monosome X, but could have been obtained from any $F_3$ families other than those segregating monosome IX.
† Significant at the 5 per cent level.
†† Significant at the 1 per cent level.

Segregation in $F_2$ families in 1947, with the exception of families involving chromosome IV, closely approached a ratio of one resistant: two intermediate: one susceptible, indicating that a single gene pair was determining the reaction. While the population in which chromosome IV was tested was small, the results indicated that the gene conditioning reaction to leaf rust was carried by this chromosome. If that were the case, the gene for resistance in Chinese Spring should have been entirely absent, and the three plants classified as resistant in this family could have been escapes.

The $F_2$ families and $F_3$ lines which were used for testing chromosome IV in 1948, did not, however, substantiate the 1947 findings. Actually, both generations gave normal monohybrid segregation in 1948.

*Reaction to Bunt, Race T-16*

The data on reaction to bunt, Race T-16, in $F_2$ and $F_3$ populations of the crosses of the 17 deficient lines of Chinese Spring with Federation 41, and in $F_2$ populations of the crosses with Hymar are summarized in Table 10.

In crosses of Hymar, a 3 : 1 ratio of resistant to susceptible plants was obtained in $F_2$ families involving all 17 chromosomes tested. If the Martin gene for resistance had been carried by one of the 17 chromosomes tested,

TABLE 9.—SEGREGATION FOR LEAF RUST REACTION IN $F_2$ AND $F_3$ POPULATIONS OF CROSSES OF FEDERATION 41 ON THE 17 DIFFERENT MONOSOMIC (OR CORRESPONDING NULLISOMIC) LINES OF CHINESE SPRING

| Chromosome tested | Reaction of plants or lines | | | Total | $X^2$ for ratio of 1 : 2 : 1 |
|---|---|---|---|---|---|
| | Resistant | Intermediate ($F_2$) Segregating ($F_3$) | Susceptible | | |
| | No. | No. | No. | No. | |
| I | 73 | 152 | 74 | 299 | 0.08 |
| II | 97 | 170 | 82 | 349 | 1.53 |
| III | 68 | 157 | 84 | 309 | 1.73 |
| IV | 3 | 23 | 24 | 50 | 18.89† |
| IV* | 77 | — | 193 | 270 | 1.78** |
| V | 68 | 152 | 71 | 291 | 0.64 |
| VI | 47 | 105 | 64 | 216 | 2.84 |
| VII | 53 | 104 | 56 | 213 | 0.20 |
| VIII | 57 | 108 | 55 | 220 | 0.11 |
| IX | 24 | 41 | 22 | 87 | 0.37 |
| X | 56 | 137 | 69 | 262 | 1.84 |
| XI | 76 | 134 | 59 | 269 | 1.76 |
| XV | 54 | 131 | 64 | 249 | 1.76 |
| XVI | 59 | 113 | 56 | 228 | 0.01 |
| XVII | 55 | 131 | 62 | 248 | 1.19 |
| XVIII | 53 | 93 | 42 | 188 | 1.30 |
| XIX | 49 | 98 | 54 | 201 | 0.37 |
| XX | 15 | 25 | 10 | 50 | 1.00 |
| Total $F_2$ (excluding families involving chromosome IV) | 904 | 1851 | 924 | 3679 | 0.37 |
| IV*** | 20 | 38 | 21 | 79 | 0.17 |

* Data from 1948. In this year the infection was more severe than in 1947 and no intermediate $F_2$ condition could be recognized.

** Ratio of 1 : 3 instead of 1 : 2 : 1.

*** $F_3$ lines instead of $F_2$ plants.

† Significant at the 1 per cent level.

except for the nullisomics, the entire $F_2$ family of the particular chromosome would have been resistant.

Segregation for reaction to bunt in $F_2$ populations derived from crosses of the 17 deficient lines of Chinese Spring with Federation 41 was different from that in populations of the Hymar crosses. With the exception of families involving chromosome XVI, segregation closely approached a ratio of 11 resistant: five susceptible plants. In families involving chromosome XVI the ratio obtained was as would be expected if the Martin gene alone were segregating. These results indicate that in the Federation 41 crosses a gene with a modifying effect on the Martin gene was present. This gene was associated with chromosome XVI as indicated by $F_2$ and $F_3$ data.

## DISCUSSION

Conventional genetic methods have resulted in very slow and limited progress in developing linkage maps of chromosomes in common wheat. The difficulties encountered in attempting such studies probably stem largely from the fact that the species is polyploid, and from the paucity of easily classifiable characters.

TABLE 10.—SEGREGATION FOR REACTION TO BUNT, RACE T-16, IN $F_2$ AND $F_3$ POPULATIONS OF CROSSES OF FEDERATION 41, AND $F_2$ POPULATIONS OF THE CROSSES OF HYMAR ON THE 17 DIFFERENT MONOSOMIC (OR CORRESPONDING NULLISOMIC) LINES OF CHINESE SPRING

| Chromosome tested | Federation 41 crosses | | | | Hymar crosses | | | |
|---|---|---|---|---|---|---|---|---|
| | Reaction of plants (lines in $F_3$) | | | $X^2$ for † 3 : 1 $F_2$ or 1 : 2 $F_3$ ratio | Reaction of plants | | | $X^2$ 3 : 1 $F_2$ ratio |
| | Resistant | Susceptible (Segregating in $F_3$) | Total | | Resistant | Susceptible | Total | |
| | No. | No. | No. | | No. | No. | No. | |
| I | 431 | 190 | 621 | 34.00** | 52 | 14 | 66 | 0.03 |
| II | 605 | 222 | 827 | 14.80** | 185 | 40 | 225 | 2.24 |
| III | 634 | 235 | 869 | 17.24** | 204 | 62 | 266 | 0.40 |
| IV | 565 | 236 | 801 | 33.59** | 93 | 34 | 127 | 2.05 |
| V | 591 | 240 | 831 | 29.77** | 168 | 53 | 221 | 0.77 |
| VI | 693 | 275 | 968 | 30.17** | 184 | 68 | 252 | 4.76* |
| VII | 635 | 246 | 881 | 24.04** | 60 | 18 | 78 | 0.08 |
| VIII | 648 | 252 | 900 | 24.77** | 391 | 121 | 512 | 1.26 |
| IX | 225 | 96 | 321 | 14.95** | 460 | 136 | 596 | 0.44 |
| X | 781 | 318 | 1099 | 40.14** | 310 | 107 | 417 | 4.48 |
| XI | 869 | 322 | 1191 | 23.44** | 303 | 99 | 402 | 2.32 |
| XV | 668 | 248 | 916 | 18.28** | 239 | 78 | 317 | 1.84 |
| XVI | 485 | 124 | 609 | 0.83 | 202 | 68 | 270 | 2.24 |
| XVII | 1175 | 530 | 1705 | 93.56** | 275 | 81 | 356 | 0.25 |
| XVIII | 551 | 202 | 753 | 13.68** | 125 | 40 | 165 | 0.77 |
| XIX | 645 | 253 | 898 | 26.12** | 159 | 46 | 205 | 0.07 |
| XX | 310 | 143 | 453 | 30.76** | 152 | 37 | 189 | 0.64 |
| Total $F_2$ (excluding families involving chromosome XVI) | 10,026 | 4008 | 14,034 | 459.03** | 3562 | 1102 | 4664 | 11.56** |
| XVI†† | 26 | 54 | 80 | 0.05 | | | | |

† Chinese Spring had 13 per cent escapes. This figure was used as a correction factor. Chi-squares were computed on the corrected results.
†† $F_3$ lines instead of $F_2$ plants. No homozygous susceptible $F_3$ lines expected, since susceptible $F_2$ plants (except escapes) had no seed.
* Significant at the 5 per cent level.
** Significant at the 1 per cent level.

Seven genes were associated with different chromosomes in this study. It should be pointed out that genes are not tested against linkage testers, but against whole chromosomes when nullisomics or monosomics are used. Thus, it is possible to associate with a certain chromosome genes that are more than 50 crossover units apart, in which case the conventional method would fail to reveal linkage.

The use of these aberrations simplifies considerably the genetic analysis of characters controlled by multiple genes. This was shown in the study of awning where unusual segregation occurred in families involving three different chromosomes, thus indicating that at least three gene pairs affected awning. In the study of habit of growth it was possible to associate one of the duplicate recessive genes for winter habit of growth in Hymar with a particular chromosome. In families involving chromosome IX, only the dominant allele of Chinese Spring, not associated with this chromosome, was segregating. This resulted in a modification of the duplicate gene $F_2$ ratio of 15 : 1, to a monohybrid 3 : 1 ratio. Had the second recessive gene been carried by one of the other 16 chromosomes tested, a similarly modified ratio would have occurred in the families of the chromosome involved. Whether or not the same results would be obtained with other duplicate recessive genes is not known.

While the Martin gene for resistance to bunt, or the gene conditioning reaction to leaf rust, was not associated with a particular chromosome, it is significant that a gene with a modifying effect on the Martin gene was associated with a particular chromosome in the study of smut reaction in the Federation 41 crosses. Whether this is the same gene, or locus, that was involved in the studies reported by Briggs (7, 8, 9), and Churchward (11), where modifiers were operating, cannot be ascertained at this time.

Cytological studies together with genetic analysis will be needed to guard against the drawing of erroneous conclusions should certain types of aberrations be encountered. Common wheat undoubtedly has many reduplicated segments of chromosomes (as do other polyploid species), and it should be recognized that univalent chromosomes might become involved in reciprocal translocations with chromosomes that are partially homologous. The resulting chromosomes would have changed genetic constitutions, and the association of a gene with a certain chromosome could be erroneous if such a gene was carried by one of the chromosomes involved in the interchange. The relative instability of univalent chromosomes results in another type of difficulty. Misdivision, especially common in univalent chromosomes (cf. Review of Literature), can result in telocentric chromosomes and isochromosomes which might seriously affect the results obtained. If, in the study of spike density, the chromosome arm carrying the recessive allele had been retained, it is doubtful if segregation in families involving chromosome XX would have differed markedly from that in families involving the other 16 chromosomes, since telocentric chromosomes in common wheat appear to be transmitted to approximately as many progeny as are normal chromosomes.

Mutant characters can be obtained in common wheat with difficulty (i.e. in low frequencies) as a result of irradiation. They can be produced with a considerably higher frequency in durum wheat, but many would

undoubtedly be concealed or "covered" by duplicate genes should an effort be made to transfer such characters from the durum to common wheat. Thus, there appears to be no simple easy way in which a large number of easily classifiable, simply inherited characters could be obtained for cytogenetic study.

The sterility of nullisomics, and the high percentage of natural crossing on such plants, might well lead to difficulties in classification and erroneous conclusions, especially if natural crosses could not be distinguished phenotypically. In two phases of this study there was evidence of high percentage of natural crossing.

It seems imperative that cytologic studies should supplement the genetic studies if these deficiencies are used. Undoubtedly further studies with these deficiencies should be undertaken, since the results of this study indicate that more definite genetic and cytogenetic information can be obtained than by the conventional methods hitherto used.

## SUMMARY

Seventeen monosomic (or corresponding nullisomic) lines of common wheat, var. Chinese Spring, were tested for their effect on the transmission of genes that distinguished this variety from two other (male parent) varieties, Hymar and Federation 41. Seven of the nine genes studied were associated with particular chromosomes.

1. The dominant gene for red colour of glumes in Federation 41 was associated with chromosome I.

2. Winter habit of growth in Hymar was conditioned by duplicate recessive genes, one of which was associated with chromosome IX.

3. Although Chinese Spring and Hymar are both almost awnless, awned $F_2$ plants were obtained. Awning in this cross was apparently conditioned by three genes. Recessive alleles of the two dominant awn-inhibiting genes of Chinese Spring were associated with chromosome VIII and X of Hymar. A dominant awn-inhibiting gene with greater effect than either of the two Chinese Spring awn inhibitors was associated with chromosome IX in Hymar. These results supplement the findings of Sears (52), and O'Mara (42).

4. Chinese Spring and Federation 41 differed by one gene pair in their reaction to leaf rust. This gene pair was not associated with any of the 17 chromosomes tested.

5. The Martin gene for resistance to bunt was not associated with a particular chromosome in either cross. In the crosses with Federation 41, a gene which modified the effectiveness of the Martin gene was associated with chromosome XVI.

6. The dense spikes of Hymar were found to be conditioned by one main dominant gene pair which was associated with chromosome XX. However, transgressive segregation indicated that at least one additional gene was modifying the degree of density or laxity of spikes.

7. A telocentric chromosome, presumably consisting of one arm of chromosome XX in both heterozygous and homozygous condition, was found in a number of $F_3$ lines of the Hymar crosses. It was not homologous

with the arm of chromosome XX which carried the gene for spike density, and was evidently present in the original female parent plant used in making the cross.

8. The advantages and limitations of monosomic (or nullisomic) lines, for cytogenetic studies have been discussed.

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# NOTE ON THE SUSCEPTIBILITY OF QUEEN AND WORKER LARVAE OF THE HONEYBEE TO AMERICAN FOULBROOD[1]

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Worker larvae of the honeybee are most susceptible to American foulbrood during the first day of larval life after which susceptibility decreases until at about two days and five hours after hatching they can no longer be infected (1, 4, 5). This period of susceptibility corresponds roughly with the period of feeding of the larvae with royal jelly (1, 4); thereafter they are fed honey and pollen. This well recognized fact suggests that infection or perhaps spore germination may be related in some manner to the royal jelly consumed. If this is true, then queen larvae which are fed royal jelly exclusively should remain susceptible over their entire larval period or at least for an appreciably longer time than worker larvae. It is well established that queen larvae are susceptible to American foulbrood (3, 5) but no attempt has been made to determine their age of susceptibility. Studies were therefore initiated with both queen and worker larvae to obtain information on this point.

## EXPERIMENTAL

Brood combs were placed in nuclei for six hours after which the combs containing eggs were either left in dequeened nuclei or removed and placed above a queen excluder in normal colonies for three days. At 6-hour intervals thereafter combs were removed and the larvae sprayed with a suspension of AFB spores so that the brood area of each comb received about one billion spores. The combs were then returned to queenless nuclei or to normal colonies above a queen excluder. A considerable number of larvae were removed from these combs by the bees; consequently, when the brood was capped, the combs were transferred to an incubator maintained at 90°-92° F. until emerging time, when each cell was examined. Diseased material was removed for microscopic examination and culturing (2). The results of two experiments, one with larvae 0–54 hours old (in dequeened nuclei) and one with larvae 48–108 hours old (kept above a queen excluder), are assembled in Table 1. It is interesting to note that many queen cells were developed in the dequeened nuclei and were thus available for comparison with worker larvae. Since many larvae had been removed from most of the combs no attempt was made to calculate the percentage of infection. It is quite obvious that both worker and queen larvae were susceptible up to 54 hours; these results agree very closely with those of Woodrow (4) with sprayed larvae.

Difficulty was experienced in the studies with queen larvae owing to extensive removal of sprayed and, to some extent, of inoculated larvae. In the first series, 12 larvae, 0–14 hours old, were grafted on each of five bars and each bar sprayed with a suspension of 100 million spores at the time intervals given in Table 2. In the second series 60 worker larvae (20–48 hours old) were grafted on six bars and left in cell-building colonies for 24 hours. They were then removed and new larvae of selected age

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TABLE 1.—SUSCEPTIBILITY OF HONEYBEE LARVAE TO AMERICAN FOULBROOD

| Larval age (hours) | Number of capped cells | Number of diseased larvae |
|---|---|---|
| 0 – 6 | 20 (2 queen) | 2 queen |
| 6 – 12 | 10 (1 drone) | 1 drone, 1 worker |
| 12 – 18 | 12 | 2 worker |
| 12 – 24 | 68 (5 queen) | 3 queen, 15 worker |
| 24 – 30 | 1 (queen) | 1 queen |
| 30 – 36 | 3 (3 queen) | 1 queen |
| 36 – 42 | 10 (7 queen) | 4 queen, 3 worker |
| 42 – 48 | 36 (3 queen) | 3 queen, 15 worker |
| 48 – 54 | 56 (6 queen) | 3 queen, 25 worker |
| 18 – 24 (check) | 45 | 43 |
| 48 – 54 | 111 | 6 |
| 54 – 60 | 334 | 0 |
| 60 – 66 | 91 | 0 |
| 66 – 72 | 43 | 0 |
| 72 – 78 | 9 | 0 |
| 78 – 84 | 54 | 0 |
| 84 – 90 | 182 | 0 |
| 90 – 96 | 141 | 0 |
| 96 – 102 | 14 | 0 |
| 102 – 108 | 191 | 0 |

TABLE 2.—SUSCEPTIBILITY OF QUEEN LARVAE OF THE HONEYBEE TO AMERICAN FOULBROOD

| Larval age (hours) | Sprayed larvae | |
|---|---|---|
| | Capped cells remaining (out of 12) | Number diseased larvae |
| 0 – 24 | 0 | — |
| 24 – 42 | 0 | — |
| 42 – 60 | 2 | 0 |
| 60 – 78 | 5 | 1 |
| 78 – 96 | 5 | 0 |
| | Individually inoculated larvae | |
| 18 – 30 | 0 | — |
| 48 – 60 | 4 | 3 |
| 60 – 72 | 10 | 1 |
| 72 – 84 | 6 | 0 |
| 84 – 96 | 10 | 0 |
| 96 – 108 | | 0 |

(18–30 hours) were grafted. The individual larvae were inoculated with one platinum loopful (2 mm. diam.) of a heavy suspension of spore material placed on the royal jelly near the mouth parts, at given intervals (Table 2); they were then returned to the colonies. Most of the sprayed larvae, as well as some of the inoculated larvae, were removed by the bees shortly thereafter. The capped cells were therefore removed to the incubator and examined at emerging time. It will be noted that of the few larvae remaining in the sprayed set one, 60–78 hours old, was infected. Results with larvae inoculated individually were more satisfactory; three of four cells

(48–60 hours old) and one out of 10 cells (60–72 hours old) were susceptible. It would seem that queen larvae are slightly more susceptible than worker larvae which could not be infected beyond the age of 54 hours. However, considering the possible variation in age of larvae selected for infection, as observed by Woodrow (4, 5), it is questionable whether the time difference involved is significant. It is quite possible, for example, that the susceptible queen larvae in the 60–72 hour set was 60 rather than 72 hours old. It appears therefore that continuous feeding on royal jelly has no appreciable influence on susceptibility of larvae to American foulbrood. This phenomenon may be associated more intimately with physiological or other changes which the larva undergoes during its third day of growth.

## SUMMARY

Studies were initiated to compare the age of susceptibility to American foulbrood of worker larvae and queen larvae of the honeybee and thereby to determine if continuous feeding on royal jelly affects susceptibility.

Worker larvae sprayed with AFB spores at 6-hour intervals from 0 to 108 hours were found to be susceptible up to but not beyond 54 hours.

Queen larvae, individually inoculated with AFB spores, were susceptible between the age limits of 48–60 hours; one out of 10 larvae 60–72 hours old was also infected.

Considering the possible variation in age of larvae selected for experimentation it was concluded that there was no significant difference between the ages of susceptibility of queen and worker larvae, and therefore that continuous feeding on royal jelly does not appear to affect susceptibility to AFB.

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